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BIOCHEMICAL STUDIES AND ENERGETICS OF THE SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS, 1758)

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MAY 2002

Dedicated to
My
Beloved Parents

कृ अनु प
C A R

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CERTIFICATE

Certified that the thesis entitled **"BIOCHEMICAL STUDIES AND ENERGETICS OF THE SPINY LOBSTER *PANULIRUS HOMARUS*"** is a record of independent bonafide research work carried out by **Mr. ANILKUMAR, P. K.** during the period of study from September 1997 to April 2002 under our supervision and guidance for the degree of **Doctor of Philosophy in Fish and Fisheries Science (Mariculture)** and the thesis has not previously formed the basis for the award of any degree, diploma, associateship, fellowship or any other similar title.

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DECLARATION

I hereby declare that the thesis entitled "**BIOCHEMICAL STUDIES AND ENERGETICS OF THE SPINY LOBSTER *PANULIRUS HOMARUS* (LINNAEUS, 1758)**" is an authentic record of the work done by me and that no part thereof has been presented for the award of any degree, diploma, associateship, fellowship or any other similar title.

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सारांश

चेन्नै मात्स्यिकी पोताश्रय में फरवरी 1999 और जनवरी 2000 के बीच शूली महा चिंगट की पकड 5532 कि ग्रा थी जिसमें 77.6% *पान्युलिरस होमारस* थे. पकडे गए शूली महा चिंगटों की पूंछ की पेशी में प्रोटीन, लिपिड, कार्बोहाइड्रेट और ऊर्जा की मात्रा क्रमशः 312.3 कि ग्रा, 41.4 कि ग्रा, 6.4 कि ग्रा और 8.1×10^6 के जे थी . *पी. होमारस* में, अध्ययन किए गए ऊतकों में (पूंछ की पेशी, हेपाटोपानक्रियास और एक्सोस्केल्टन) , हेपाटोपानक्रियास में उच्चतम ऊर्जा (24.6 ± 0.7 के जे / ग्रा) और लिपिड मात्रा (31.6 ±1.8%) देखी गई. *पी.होमारस* के किशोरों (50 - 100 ग्रा शरीर भार) और प्रौढ़ों (150 - 200 ग्रा शरीर भार) के बीच निकट संयोजन और ऊर्जा की मात्रा में मौसमिक परिवर्तन की कोई विशिष्ट प्रवणता भी नहीं थी. भूख के प्रभाव पर किए गए परीक्षण में यह देखा गया कि नियंत्रित अवस्था के और नेत्रवृंत अपक्षरण किए गए *पी. होमारस* क्रमशः 970±5.3 और 48.3 ± 4.8 दिनों तक ज़िंदा रहे. भूख की वजह से भार क्षय नियंत्रित अवस्था में पूर्व भार का 37.1% और अपक्षरण की अवस्था में 51.6% देखा गया. मृत्यु के वक्त *पी.होमारस* में सूखे हेपाटोसोमाटिक इन्डेक्स (HSI_d) 1.75% से 4.72% तक (नियंत्रित) और 1.64% तक (अपक्षरण) घट गया. भूख से सभी जैवरासायनिक घटकों की कमी हुई और लिपिड ऊर्जा का प्रमुख श्रोत था. नियंत्रित और अपक्षरण किए गए ग्रुपों में होपाटोपानक्रियास में प्रोटीन ऊर्जा के अनुपात में क्रमशः 0.0903 से 0.1342 और 0.1471 तक परिवर्तन देखा गया. *पी. होमारस* की अधिकतम बढ़ती दर प्राप्त करने केलिए खाद्य उपयोगिता प्राचल पर चार प्राकृतिक खाद्यों जैसे चिंगट, स्क्विड, सीपी और शंबु के प्रभाव पर अध्ययन किया गया. शंबु खिलाए गए ग्रुप में उच्चतम भोजन दर (263.5 ± 20.3 जे/जी/डी) देखी गई बल्कि अधिकतम परिरक्षणदर(23.9+1.0 जे/डी निर्मोचन के अतिरिक्त) सीपी खिलाए गए ग्रुप में देखी गई. दो निर्मोचनों के बीच की अवधि का रेंच 42.7 ± 1.5 दिनों (सीपी खिलाए गए) से 52.3± 2.5 दिनों तक (स्क्विड खिलाए गए) था. खाद्य परिवर्तन का अनुपात (FCR) का रेंच 2.74±0.17 (सीपी खिलाए गए) से 4.08±0.06 (स्क्विड खिलाए गए) तक था. उपभोक्त किए ऊर्जा का प्रमुख भाग (84.1 सं 87.4 %) उपापचय केलिए और 6.9 से 10.2 % बढ़ती के लिए लिया गया.

ABSTRACT

The spiny lobster landings at Chennai Fisheries Harbour was 5532 kg between February 1999 and January 2000, of which *Panulirus homarus* contributed 77.6%. The tail muscle of the landed spiny lobsters yielded 312.3 kg, 41.4 kg, 6.4 kg and 8.1 x 10^6 kj of protein, lipid, carbohydrate and energy respectively. In *P. homarus*, among the tissues studied (tail muscle, hepatopancreas and exoskeleton), the hepatopancreas had the highest energy (24.6 $\pm$ 0.7 kj/g) and lipid contents (31.6 $\pm$ 1.8%). There was no significant difference in the proximate composition and energy contents between the juvenile (body weight: 50-100 g) and maturing (body weight: 150-200 g) *P. homarus*. No specific trend in the seasonal variation was observed in the proximate composition and energy content. In the experiment on the effect of starvation, the control and bilaterally eyestalk ablated *P. homarus* survived for 97.0 $\pm$ 5.3 and 48.3 $\pm$ 4.8 days respectively. The weight loss due to starvation was 37.1% of initial wet weight in the control and 51.6% in the ablated lobsters. The dry hepatosomatic index (HSI_d) decreased from 4.72% to 1.75% (control) and 1.64% (ablated) in *P. homarus* at the time of death. All the biochemical components decreased with starvation, with lipid as the major energy source. The protein energy ratio changed from 0.0903 to 0.1342 and 0.1471 in the hepatopancreas of the control and ablated groups respectively. For achieving the maximum growth rate of *P. homarus*, the effect of four natural food *viz.*, shrimp, squid, clam and mussel on the food utilization parameters were studied. The highest feeding rate (263.5 $\pm$ 20.3 j/g/d) was observed in the mussel-fed group, but the maximum conversion rate (23.9 $\pm$ 1.0 j/g/d excluding moult) was found in the clam-fed group. The intermoult duration ranged from 42.7 $\pm$ 1.5 days (clam-fed) to 52.3 $\pm$ 2.5 days (squid-fed). The food conversion ratio (FCR) ranged between 2.74 $\pm$ 0.17 (clam-fed) to 4.08 $\pm$ 0.06 (squid-fed). A major share (84.1 to 87.4%) of the consumed energy was partitioned for metabolism and 6.9 to 10.2 % for growth.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

1. INTRODUCTION

Lobsters are typically marine and are distributed along the entire coast of India. They are commercially exploited for more than five decades. The fishery consists of eight species of spiny lobsters and two species of slipper lobsters. Of these, *Panulirus homarus* (Linnaeus, 1758), *P. polyphagus*, *P. ornatus*, *Thenus orientalis* and *Puerulus sewelli* form the main fishery (Radhakrishnan and Vijayakumaran, 1990; Kagwade, 1993; Suseelan, 1996). The annual landings of the lobsters along the Indian coast fluctuated between 2000-3000 t with a peak of 4075 t in 1985 (Vijayakumaran and Radhakrishnan, 1997). The landings were 2387 t in 2000 (CMFRI, 2001). Though the lobsters contribute only about 0.1% to the total marine fish landings along the Indian coast (Radhakrishnan and Manisseri, 2001), they enjoy lucrative export market. The current export value of the lobsters is Rs 542.7/kg amounting to Rs 896.9 million (MPEDA, 2000), which is 1.4% of the total value of the export.

The demand for spiny lobsters from the domestic as well as from the export markets is met exclusively through capture fisheries. Chennai Fisheries Harbour is one of the major fish landing centers, where there is regular landing of the spiny lobsters. Information on the monthly variations in the landings, the biochemical composition such as protein, lipid and carbohydrate and the calorific content is needed for determining the seasonal availability of lobsters and for assessing the nutritional availability through the lobster landings. Moreover, nutritional condition of lobsters, as assessed in the field, could be a valuable tool to provide an insight into the physiological responses of lobsters to environmental constraints. Though information on the fisheries and some biological aspects of the spiny lobsters occurring along the Indian coast is available, data on the seasonal variations in the landings, the biochemical composition and calorific content of the lobsters in the landings are scarce. Studies on lobster have generally centered on the needs associated with rearing and aquaculture.

Nutritional deprivation is part of the life of many aquatic organisms as the result of winter torpor, seasonal non-availability of food or behavioural modifications during mating/spawning and moulting (Claybrook, 1983; Schirf *et al.*, 1987). In the tropical waters, changes in climatic conditions and food availability are not pronounced, and hence prolonged starvation may not be a common feature among the aquatic organisms. However, starvation occurs during moulting, spawning/mating and between the time taken for digesting the ingested food. This is evidenced from the high percentage of organisms with empty stomach, which occurs regularly in the samples collected from the wild. For instance, Sukumaran and Neelakantan (1997) observed that 29.2% and 37.0% of the samples of the crabs *Portunus sanguinolentus* and *P. pelagicus,* collected from the natural population had empty stomach. Nevertheless, studies on the effects of prolonged starvation on the survival, loss of weight and changes in the energy and biochemical components are useful for determining the physiological strategies, which the organisms would adopt to negotiate the conditions of extreme stress.

Compared to several other aquatic organisms, the crustaceans may have to adopt unique strategies when exposed to extreme starvation. Whereas the aquatic organisms such as fishes restrict their activities and resort to basal metabolism (Vivekanandan, 1977), several crustaceans moult even under prolonged starvation (*Palaemon lamarrei*: Katre and Reddy, 1976; *Macrobrachium lanchesteri*: Ponnuchami *et al.*, 1981; *Metapenaeus monoceros*: Sumitra Vijayaraghavan *et al.*, 1982). Radhakrishnan (1989) reported moulting in bilaterally eyestalk ablated, starved *P. homarus*. However, starvation inhibits and slows down the process of moulting in the crustaceans (*Pachygrapsus crassipes*: Roberts, 1957; *Penaeus japonicus*: Cuzon *et al.*, 1980). Moulting may be impeded or prevented if other demands are made simultaneously on the organic reserves (Passano, 1960).

The nutritional state of animals such as crustaceans, which are enclosed in a more or less rigid integument, could not be readily

assessed by the external appearance. Starvation does not make any apparent difference to the external appearance or dimensions. Hence, it has become necessary to develop an index to find out the nutritional status of the animal. An accurate technique for measuring nutritional condition would be valuable in lobster ecology, aquaculture and enhancement of wild populations. Measurements of nutritional condition can indicate whether food or animal density is a factor limiting growth and survival or whether broodstock or captive animals intended for out-planting are in good health. A variety of condition indices have been developed in an attempt to evaluate the nutritional state of crustaceans, which includes organosomatic indices (Schrif *et al.*, 1987; Evans *et al.*, 1992; Jussila and Mannonen, 1997; Tsvetnenko *et al.*, 1999), haemolymph chemistry and refractive index (Dall, 1974; Oliver and MacDiarmid, 2000; Musgrove, 2001), glycogen content (Parrish and Martinelli, 1999), gastric fluid constituents (Dall, 1975), triacylglycerol (Fraser, 1989; Harding and Fraser, 1999), and nucleic acids (Wang and Stickle, 1986; Juinio *et al.*, 1992; Stuck *et al.*, 1996; Parslow-Williams *et al.*, 2001). Hepatopancreas or the midgut gland is a vital organ for the crustaceans, which is involved in diverse metabolic activities, and is primarily responsible for the synthesis and secretion of digestive enzymes and subsequent uptake of nutrient materials. It is also implicated in excretion, the moult cycle and the storage of organic reserves, lipid and carbohydrate metabolism. Hepatopancreas is highly sensitive to starvation and changes in the environmental conditions (Vogt *et al.*, 1985). Monitoring the biochemical changes in the hepatopancreas due to prolonged starvation is important, since the hepatopancreas could be a potential indicator organ for assessing the nutritional status of the crustaceans (Papathanassiou and King, 1984).

Of the fifty or so extant palinurids, only a few have been extensively studied by maintaining in the laboratory for any length of time and very less number of species (*Jasus lalandii*: Kittaka, 1988; *Jasus* hybrid: Kittaka *et al.*, 1988; *Palinurus elephas*: Kittaka and Ikegami, 1988; *Panulirus japonicus*: Kittaka and Kimura, 1989; Yamakava *et al.*,

1989; *J. verreauxi*: Kittaka *et al.*, 1997; *J. edwardsii*: Illingworth *et al.*, 1997) have been successfully reared through their entire life cycle. A long and complex larval life, inadequate knowledge on the nutritional needs and maintenance of high water quality standards are the major constraints in the larval rearing of the spiny lobsters. Hence, for the present, any attempt to culture the lobsters should concentrate on either long-term lobster farming *i.e.*, growing undersized lobsters (<100 g) to the preferred export size of above 200 g or short term fattening for value addition to fetch the premium price. Lobsters are priced according to the weight and are graded commercially as <100 g, 100-200 g and >200 g for *P. homarus*, *P. polyphagus* and *P. versicolor* and <500 g, 500-1000 g, 1000-2500 g and >2500 g for *P. ornatus* (CMFRI, 2001). The difference in export price between a lower grade and the next higher grade is nearly 125-150%. Therefore, short term fattening of a lower priced smaller grade to a higher priced larger grade is most profitable. The juveniles, which are being exploited regularly, contribute 35 to 40% to the commercial lobster catches in India (Radhakrishnan and Vijayakumaran, 1990). Considering the availability of the juvenile resource and high value realization, fattening of juveniles to the next higher size grade is considered as a more straightforward approach. For fattening the lobsters in the farms, an understanding of the food utilization parameters such as food consumption, absorption, growth and metabolism is essential.

Food quality has been recognized as one of the important factors that influences growth process in animals (Brown, 1957; Ford, 1977; Sedgwick, 1979; Jones *et al.*, 1995). Study on the effect of food quality on food utilization parameters would provide valuable clues on the food that could be recommended for achieving maximum growth rate. Even though the potential for lobster fattening is vast, only limited attempt has been made so far to identify the food that provides maximum growth rate by optimising the other food utilization parameters.

Extensive studies (Castell *et al.*, 1976, 1977; Mauviot and Castell, 1976; Capuzzo and Lancaster, 1979; Bayer *et al.*, 1981; D'

Abramo *et al.*, 1981; Capuzzo, 1982; Norman-Boudreau and Conklin, 1984; Bordner *et al.*, 1986; Sarvaiya, 1988; Baum *et al.*, 1990; Lellis, 1992; Bayer *et al.*, 1993; Brown *et al.*, 1995; Lim *et al.*, 1997; Donahue *et al.*, 1997, 1999; Crear *et al.*, 2000; Dias-Wanigasekera *et al.*, 2000; Floreto *et al.*, 2000a, 2001; Glencross *et al.*, 2001) are available on the effects of formulated feed on the growth of lobsters. Several of these studies have repeatedly demonstrated that pellet instability results in unrecoverable loss of diet, leading to deterioration of water quality. Moreover, pellet feed is not readily accepted by most of the spiny lobsters (Radhakrishnan, 1989). The spiny lobsters have the tendency to tear and eat the food material with the help of the mandible, and hence, pellet is not suited for their feeding behaviour. The unsuitability of pellet feeds calls for studies on the effect of natural food on the food utilization of the spiny lobsters.

Lobsters are selective of the food they eat (Phillips *et al.*, 1980). Berry (1971) observed that the diet of the spiny lobster *P. homarus* consists mostly of mussels. Chittleborough (1974a) reported that the rock lobster, *P. longipes cygnus* accepts a wide range of animals as food but prefers molluscs to fish. The proportion of food item in the stomach of the lobsters is reported to be different from the relative abundance of the food items in the habitat. For instance, the proportion of the crabs in the diet of *Homarus americanus* was higher than the relative density in the field (Weiss, 1970; Ennis, 1973). Evans and Mann (1977) observed selective feeding behaviour of *H. americanus* in the laboratory. Despite these clues on the selective feeding of the lobsters in the wild as well as in the laboratory conditions, there are only a few investigations on the effect of different food items on the food utilization of the lobsters.

In nutrition studies, it is often necessary to know the calorific value of the feed, faeces and muscle tissue. These values are necessary to compute the energy budget and to determine the efficiencies of absorption and conversion. An understanding of the energy budget of an organism is of great importance for evaluating its potential for

aquaculture. Reviewing the crustacean energetics, Vernberg (1987) stressed the need for estimating the compelete energy budget. Knowledge on bioenergetics and partition of the dietary components for catabolism, and for the growth of the lobster is necessary for optimizing the dietary regime. Successful lobster fattening depends on proffering diets containing right balance of nutrients and adequate energy that would promote most efficient growth.

The present study has been undertaken to find out i) the possiblity of a trend in the monthly spiny lobster landings and their species composition in the Chennai Fisheries Harbour; ii) the seasonal changes in the protein, lipid, carbohydrate and energy contents in two size groups of *P. homarus* off Chennai; iii) effect of starvation on the survival, loss of weight, and changes in the energy and biochemical components of normal and bilaterally eyestalk ablated *P. homarus*; iv) suitability of the dry Hepatosomatic Index (HSI_d) as an index of starvation/nutritional status; v) construction of energy budgets by offering four natural foods, *viz.*, shrimp (*Penaeus indicus*), squid (*Loligo duvauceli*), clam (*Paphia malabarica*) and mussel (*Perna viridis*); and vi) the food that provides maximum rate and efficiency of conversion in the juveniles of the spiny lobster *P. homarus*.

REVIEW OF LITERATURE

2. REVIEW OF LITERATURE

2.1 Seasonal Variation in the landings and proximate composition

2.1.1 Seasonal variations in the landings of the lobsters

The lobster fishery and its seasonal variations along the Indian coast were reported by Miyamoto and Shariff (1961); George (1967, 1973); Kagwade *et al.* (1991); Kagwade (1993); Radhakrishnan (1993); CMFRI (1997, 1998, 2000, 2001); Rajamani and Manickaraja (1997a, b); Vijayakumaran and Radhakrishnan (1997); Jadhav and Rao (1998); and Radhakrishnan and Manisseri (2001).

2.1.2 Biochemical composition of the crustaceans

There is considerable literature on the biochemical composition *viz.*, protein, lipid and carbohydrate, in different body tissues as well as in the entire body of the crustaceans collected from their natural populations. The biochemical composition has been determined in relation to moult cycle (*Emerita asiatica* and *Ligia exotica*: Parvathi, 1971a; *Penaeus japonicus*: Teshima *et al.*, 1977; *Penaeus indicus*: Read and Caulton, 1980; *Penaeus esculentus*: Barclay *et al.*, 1983; *Panulirus homarus*: Radhakrishnan, 1989; *Astacus astacus*: Huner *et al.*, 1990; *Pleoticus muelleri*: Jeckel *et al.*, 1990), maturity stages (*Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis*: Pillay and Nair, 1973; *Parapenaeopsis hardwickii*: Kulkarni and Nagabhushanam, 1979; *Penaeus indicus*: Galois, 1984; *Penaeus setiferus* and *P. aztecus*: Castille and Lawrence, 1989; *Panulirus homarus*: Vijayakumaran, 1990; *Nephrops norvegicus*: Tuck *et al.*, 1997; *Eriocheir sinensis*: Cheng *et al.*, 2000; *Penaeus vannamei*: Palacios *et al.*, 2000; *Litopeneaus vannamei*: Wouters *et al.*, 2001; *Penaeus semisulcatus*: Sivachandrabose, 2002), starvation (*Emerita asiatica* and *Ligia exotica*: Parvathi, 1971b; *Pandalus platyceros*: Whyte *et al.*, 1986), body size (*Paratelphusa guerini*: Venkatachari and Ambore, 1973; *Podopthalmus vigil*: Radhakrishnan and Natarajan, 1979), water quality parameters (*Penaeus kerathurus*:

Mourente and Rodriguez, 1997; *Farfantepenaeus californiensis*: Ocampo *et al.*, 2000; *Farfantepenaeus paulensis*: Lemos *et al.*, 2001), pathological conditions (*Homarus americanus*: Floreto *et al.*, 2000b; *Nephrops norvegicus*: Stentiford *et al.*, 2000), larval development (*Metaplax elegans*: Balagurunathan and Kannupandi, 1995) etc. (Table 1).

2.1.3 Seasonal variations in the biochemical composition of the crustaceans

The trends in the seasonal variations in the biochemical constituents such as protein, lipid and carbohydrate have been studied extensively in crustaceans. The seasonal changes in the biochemical components in the crustaceans have been related to moult cycle (*Carcinus maenas*: Heath and Barnes, 1970; *Ovalipes punctatus*: Du Preez and Mc Lachlan, 1983; *Panulirus argus*: Ferrer, 1988; *Jasus lalandii*: Cockcroft, 1997), reproduction (marine and freshwater decapods: George and Patel, 1956; *Macrobrachium borellii*: Gonzalez-Baro and Pollero, 1988; *Pleoticus muelleri*: Jeckel *et al.*, 1989a,b, 1991), temperature and nutrition (*Penaeus setiferus*, *P. aztecus* and *P. duorarum*: Bottino *et al.*, 1980; *Panulirus marginatus*: Parrish and Martinelli, 1999), wandering behaviour (*Scopimera globosa*: Iwata *et al.*, 1983), changes in haemocyanin in relation to sex (*Palinurus elephas*: Giardina *et al.*, 1986; *P. elephas* and *P. mauritanicus*: Bellelli *et al.*, 1988) etc. (Table 2).

2.2 Effect of starvation

The ability to withstand complete starvation differs from one organism to another. Number of studies are available on the effects of starvation or nutritional stress on several species of palinurid and nephropid lobsters and crayfishes (Table 3). The duration of starvation in these experiments ranges from few days (Stewart *et al.*, 1967; Anger *et al.*, 1985) to prolonged starvation lasting for several weeks (Stewart *et al.*, 1972) or upto death (Chittleborough, 1975; Radhakrishnan, 1989).

Table.1 List of important literature on the biochemical and energy contents of the crustaceans (only a few selected references are listed)

Sl. no.	Species	Parameters/ Aspects studied	Remarks	Reference
1	*Emerita asiatica* and *Ligia exotica*	Carbohydrate metabolism	Effect of starvation	Parvathi (1971b)
2	*Emerita asiatica* and *Ligia exotica*	Glycogen content	In relation to moult cycle	Parvathi (1971a)
3	*Emerita holuisi*	Biochemical composition	In the sandy beaches of southwest India	Ansell *et al.* (1973)
4	*Homarus* spp.	Lipid composition	In the nerve tissue	Noren and Svennerholm (1973)
5	*Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis*	Biochemical composition	In the gonads and hepatopancreas during the reproductive cycle	Pillay and Nair (1973)
6	*Paratelphusa guerini*	Protein composition	In different tissues with sex and size	Venkatachari and Ambore (1973)
7	*Chionoecetes opilio*, *Cancer borealis* and *Geryon quinquedens*	Biochemical composition	In the edible tissues	Lauer *et al.* (1974)
8	*Penaeus japonicus*	Lipid classes	During the moult cycle	Teshima *et al.* (1977)
9	*Parapenaeopsis hardwickii*	Organic reserves	During the ovarian development	Kulkarni and Nagabhushanam (1979)
10	*Podopthalmus vigil*	Biochemical composition	In relation to size	Radhakrishnan and Natarajan (1979)
11	*Euphausia superba*	Biochemical composition	From South Georgia	Clarke (1980)
12	*Penaeus indicus*	Biochemical composition	During moult cycle and ovarian development	Read and Caulton (1980)
13	*Aristaeomorpha foliacea* and *Heterocarpus dorsalis*	Lipid content	Comparison between muscle and carapace	Burgos Gonzalez and Fernadez Aguado (1981)
14	*Penaeus esculentus*	Protein and lipid content	During the moult cycle and starvation	Barclay *et al.* (1983)

15	*Penaeus indicus*	Lipid content	Due to vitellogenesis	Galois (1984)
16	*Pandalus platyceros*	Biochemical composition	With reference to starvation	Whyte *et al.* (1986)
17	*Penaeus setiferus* and *P. aztecus*	Biochemical composition	In gonads and digestive gland with reference to maturation	Castille and Lawrence (1989)
18	*Panulirus homarus*	Biochemical composition and energy content	With reference to moulting	Radhakrishnan (1989)
19	*Astacus astacus*	Biochemical composition	As a function of moult and reproductive cycle	Huner *et al.* (1990)
20	*Pleoticus muelleri*	Biochemical composition	In the hepatopacreas of females during moult cycle	Jeckel *et al.* (1990)
21	*Panulirus homarus*	Biochemical composition and energy content	With reference to maturity	Vijayakumaran (1990)
22	*Scylla serrata*	Biochemical composition	In the muscle	Mathai and Devi (1993)
23	*Penaeus monodon*	Biochemical composition	In exuvia and whole body	Sarac *et al.* (1994)
24	*Metaplax elegans*	Biochemical composition	During larval development	Balagurunathan and Kannupandi (1995)
25	*Penaeus kerathurus*	Lipid composition	Effect of salinity and dietary DHA	Mourente and Rodriguez (1997)
26	*Nephrops norvegicus*	Biochemical composition	With ovarian maturation	Tuck *et al.* (1997)
27	*Homarus americanus*	Protein	From arthrodial meberane	Andersen (1998)
28	*Scylla serrata*	Protein and carbohydrate	Effect of naphthalene	Elumalai *et al.* (1998)
29	*Heterocarpus vicarius*	Biochemical composition	From Gulf of California	Hendrickx *et al.* (1998)
30	*Portunus pelagicus, P. sanguinolentus, Charybdis cruciata* and *C. lucifera*	Biochemical composition	Comparison between different species	Selvin *et al.* (1998)

31	*Jasus edwardsii*	Biochemical composition	Comparision between the onshore and offshore pueruli	Jeffs *et al.* (1999)
32	*Panulirus cygnus*	Lipid	As a condition index of nutritional state	Tsvetnenko *et al.* (1999)
33	*Eriocheir sinensis*	Lipid	Effect of ovarian maturation	Cheng *et al.* (2000)
34	*Homarus americanus*	Biochemical composition	In shell diseased lobster	Floreto *et al.* (2000b)
35	*Macrobrachium rosenbergii*, *Penaeus indicus* and *Thenus orientalis*	Biochemical composition	In common fish and shellfish from Indian waters	Nair and Mathew (2000)
36	*Farfantepenaeus californiensis*	Biochemical composition	With temperature and dissolved oxygen	Ocampo *et al.* (2000)
37	*Penaeus vannamei*	Biochemical composition	In ovary, hepatopancreas and haemolymph related to multiple spawing	Palacios *et al.* (2000)
38	*Barytelphusa guerini*	Carbohydrate metabolism	Effect of trivalent and hexavalent chromium	Sridevi and Reddy (2000)
39	*Nephrops norvegicus*	Biochemical composition	Hematodinium infection in deep abdominal flexor muscle	Stentiford *et al.* (2000)
40	*Farfantepenaeus paulensis*	Biochemical composition and energy content	In postlarvae at different salinities	Lemos *et al.* (2001)
41	*Litopenaeus vannamei*	Lipid composition	In different reproductive stages from the wild	Wouters *et al.* (2001)
42	*Macrobrachium rosenbergii*	Biochemical composition	From two different culture systems	Rajeev (2002)
43	*Macrobrachium rosenbergii*	Biochemical composition	In PL fed with cladoceran	Safiullah and Altaff (2002)

44	*Penaeus semisulcatus*	Biochemical composition	During different vitellogenic phases	Sivachandrabose (2002)

Table.2 List of important literature on the seasonal variation in the biochemical and energy contents of crustaceans (only a few selected references are listed)

Sl. no.	Species	Parameters/ Aspects studied	Remarks	Reference
1	Marine and freshwater decapods	Lipid content	In the hepatopancreas and gonads	George and Patel (1956)
2	*Callinectes sapidus*	Amino acid composition	Nil	Thompson and Farragut (1966)
3	*Carcinus maenas*	Biochemical composition	In relation to moult cycle	Heath and Barnes (1970)
4	*Homarus americanus*	Serum protein	Off Bonavista Bay	Ennis (1973)
5	*Penaeus japonicus*	Lipid composition	Nil	Guary *et al.* (1974)
6	*Chorismus antarticus*	Lipid content	At South Georgia	Clarke (1977)
7	*Taphromysis bowmani*	Biochemical composition and energy content	Nil	Johnson and Hopkins (1978)
8	*Neptunus pelagicus* and *Scylla serrata*	Glycogen, lipid and cholestrol contents	Along the Saurashtra coast	Senthikumar and Desai (1978)
9	Gulf of Mexico shrimp	Fatty acid content	Nil	Lilly (1979)
10	*Penaeus setiferus*, *P. aztecus* and *P. duorarum*	Fatty acid content	Effects of temperature and nutrition	Bottino *et al.* (1980)
11	*Ovalipes punctatus*	Biochemical composition	With reference to moulting, reproduction, and/or changes in prey species	Du Preez and Mc Lachlan (1983)
12	*Scopimera globosa*	Glycogen and lipid contents	With reference to wandering behaviour	Iwata *et al.* (1983)
13	*Penaeus semisulcatus*	Biochemical composition	Nil	Nuwayhid and Young (1985)
14	*Palinurus elephas*	Haemocyanin	In relation to sex	Giardina *et al.* (1986)
15	*Palinurus elephas* and *P. mauritanicus*	Haemocyanin	In relation to sex	Bellelli *et al.* (1988)

16	*Panulirus argus*	Phenol oxidase	In relation to moult	Ferrer (1988)
17	*Macrobrachium borellii*	Lipid content and classes	In the muscle, hepatopancras and gonads	Gonzalez-Baro and Pollero (1988)
18	*Pleoticus muelleri*	Lipid classes	In the ovary	Jeckel *et al.* (1989a)
19	*Pleoticus muelleri*	Distribution of fatty acids	In the testes	Jeckel *et al.* (1989b)
20	*Pleoticus muelleri*	Biochemical composition, lipid class and fatty acids	In the hepatopancreas related to physiological and ecological factors	Jeckel *et al.* (1991)
21	*Jasus lalandii*	Biochemical composition	In the hepatopancreas and abdominal muscle of males in relation with moulting	Cockcroft (1997)
22	*Panulirus marginatus*	Glycogen	In the abdominal muscle of males	Parrish and Martinelli (1999)

Table 3. List of important literature on the effects of starvation on the lobsters and crayfishes

Sl. no.	Species	Parameters/ Aspects studied	Remarks	Reference
Survival				
1	*Cherax destructor*	Survival	Nil	Frost (1974)
2	*Cherax destructor*	Survival	Nil	Lake and Sokol (1986)
3	*Panulirus longipes*	Survival	Nil	Chittleborough (1975)
4	*Homarus americanus*	Survival, moult cycle and ultrastructure of hepatopancreas	Stage I larvae	*Anger et al.* (1985)
5	*Homarus americanus*	Survival	Postlarvae	Juinio *et al.* (1992)
6	*Homarus americanus*, *Jasus verreauxi* and *J. edwardsii*	Survival, moulting	First larvae and phyllosoma	Abrunhosa and Kittaka (1997a)
Biochemical composition, water and energy contents				
7	*Homarus americanus*	Protein, lipid, acidic carbohydrate, glycogen, hepatosomatic index, haemocyte count	In serum and hepatopancreas; biochemical composition in hepatopancreas determined by histochemistry	Stewart *et al.* (1967)
8	*Orconectes virilis*	Glycogen metabolism	Freshwater crayfish	Jungreis (1968)
9	*Orconectes limosus*	Biochemical composition	Freshwater crayfish	Speck and Urich (1969)
10	Crayfish	Metabolic reserves	Mobilization pattern	Chaisemartin (1971)
11	*Homarus americanus*	Protein, lipid, carbohydrate, lactic acid, non protein nitrogen, glycogen, water and hepatosomatic index	In the serum and hepatopancreas	Stewart *et al.* (1972)

12	*Panulirus longipes*	Protein, carbohydrate, glucose, water, non protein amino acid, copper and blood volume	In the blood, leg muscle, tail muscle and hepatopancreas	Dall (1974)
13	*Orconectes virilis*	Energy reserves, aggression and locomotion	Nil	Hazlett *et al.* (1975)
14	*Nephropus norvegicus*	Size and lipid	In the hepatopancreas	Dall (1981)
15	*Orconectes nais*	Water and lipid	At different temperature regimes	Armitage and Wall (1982)
16	*Astacus astacus*	Lipid and glycogen	In the hepatopancreas and abdomen	Huner *et al.* (1985)
17	*Homarus americanus*	Dry mass	During development	Sasaki *et al.* (1986)
18	*Procambarus clarkii*	Energy metabolism	In the . hepatopancreas and tail muscle	Schirf *et al.* (1987)
19	*Panulirus homarus*	Survival, weight loss, moulting, metabolic rate, water, ash and energy	In normal and eyestalk ablated lobster	Radhakrishnan (1989)
20	*Cherax tenuimanus*	Hepatosomatic index and muscle carbohydrate	As an index of nutritional condition	Evans *et al.* (1992)
21	*Homarus americanus*	Thickness, distribution pattern and relative number of various cell types	In the hepatopancreas	Niles *et al.* (1993)
22	*Cherax destructor*	Size and nutrient content	In the hepatopancreas	Jones and Obst (2000)
Metabolism				
23	*Panulirus argus*	Oxygen consumption and nitrogen excretion	Postlarvae and juvenile	Conceicao *et al.* (1996)

Most of these studies have concentrated on the effects of starvation on the survival, biochemical composition, moult cycle, metabolism, hepatosomatic index and hepatopancratic cell structure. The literature on biochemical composition concentrates on the quantitative and qualitative changes in the protein, lipid and carbohydrate contents in addition to water, ash and energy contents in various body tissues especially in the hepatopancreas of the lobsters.

Among the palinurid lobsters, the effect of starvation has been studied in 3 species, namely, *P. homarus* (Radhakrishnan, 1989), *P. longipes* (Dall, 1974; Chittleborough, 1975) and *P. argus* (Conceicao *et al.*, 1996). Of these, the one on *P. homarus* (Radhakrishnan, 1989) is the only study available on the Indian spiny lobster. Radhakrishnan (1989) studied the survival, food utilization parameters, water, ash and energy contents in the whole body of the normal and bilaterally eyestalk ablated lobsters but did not estimate the changes in the biochemical components such as protein, lipid and carbohydrate.

2.3 Effect of different food on food utilization

Several estimates are available on food utilization parameters of the lobsters under captivity. Under captive conditions, several parameters such as growth, frequency and duration of moulting, food consumption, faecal and nitrogenous wastes and respiration have been estimated for a number of species (Table 4). Nevertheless, growth and food consumption are the dominant parameters that have been often estimated and information on excretion is scanty. The food utilization parameters have been estimated by exposing the lobsters to different environmental conditions such as temperature, salinity, dissolved oxygen etc., as well as to different biotic conditions such as eyestalk ablation, quantitative and qualitative food availability, feeding schedule etc.

The energy budget has been constructed for *Homarus americanus* (Miller *et al.*, 1971; Logan and Epifanio, 1978), *Jasus lalandii* (Barkai and Branch, 1988) and *P. homarus* (Radhakrishnan, 1989;

Table 4. List of important literature on food utilization parameters of lobsters based on laboratory experiments and in growouts

Sl. no.	Species	Parameters/ Aspects studied	Remarks	Reference
1	*Panulirus argus*	Growth	Increase in size	Travis (1954)
2	*Homarus americanus*	Growth and moulting	Held for as long as 10 years	Hughes and Matthiessen (1962)
3	*Jasus lalandii*	Growth	Nil	Fielder (1964)
4	*Panulirus cygnus, Jasus novaehollandiae* and *J. verreauxii*	Carapace length increment	Nil	Chittleborough (1967)
5	*Homarus americanus*	Growth	Effect of space on growth	Mc Leese (1972)
6	*Panulirus homarus*	Growth	Nil	Thomas (1972)
7	*Panulirus polyphagus*	Growth	Effect of antennal regeneration on growth	Kathirvel (1973)
8	*Homarus americanus*	Growth	Effect of dietary protein level on growth	Castell and Budson (1974)
9	*Panulirus longipes cygnus*	Growth	From puerulus to adult	Chittleborough (1974b)
10	*Homarus vulgaris*	Growth and moulting	Reared for one year at 10^0 C	Hewett (1974)
11	*Homarus americanus*	Growth	Effect of feeding frequency and space on growth	Shleser (1974)
12	*Homarus americanus*	Growth	Effect of dietary cholestrol	Castell *et al.* (1975)
13	*Panulirus longipes cygnus*	Growth and survival	Effect of temperature, photoperiod, oxygen and food supply	Chittleborough (1975)
14	*Homarus gammarus*	Growth and survival	Effect of temperature	Danielssen and Iversen (1975)
15	*Homarus americanus*	Growth and survival	Effect of space	Sastry *et al.* (1975)

16	*Panulirus interruptus*	Growth	Culture at elevated temperatures	Serfling and Ford (1975)
18	*Homarus americanus*	Growth	In relation to eyestalk ablation	Castell *et al.* (1976)
19	*Panulirus longipes cygnus*	Growth	Comparison between wild and captive lobsters	Chittleborough (1976)
20	*Homarus americanus*	Moulting and growth	Effect of eyestalk ablation	Mauviot and Castell (1976)
21	*Homarus americanus*	Moulting and Growth	Nil	Aiken (1977)
22	*Panulirus longipes*	Growth	Fed on *Mytilus edulis*, *Haliotis roei* and teleosts	Phillips *et al.* (1977)
23	*Homarus americanus*	Growth	Nil	Sastry and French (1977)
24	*Homarus americanus*	Growth	Effect of space and density	Aiken and Waddy (1978)
25	*Homarus americanus H. gammarus* and their hybrid	Growth	Juveniles fed on adult brine shrimp	Carlberg *et al.* (1978)
26	*Homarus americanus*	Growth and conversion efficiency	Effect of temperature and feeding level	Bartley *et al.* (1980)
27	*Panulirus argus*	Moult and gonadal development	Effect of eyestalk ablation	Quackenbush and Herrinkind (1981)
28	*Panulirus homarus*	Growth	Effect of eyestalk ablation	Silas (1982)
29	*Panulirus homarus*	Growth	Effect of eyestalk ablation	Radhakrishnan and Vijayakumaran (1982)
30	*Panulirus homarus*	Growth	Marine cages	Srikrishnadhas *et al.* (1983)
31	*Homarus* sp.	Growth	With formulated diets	Norman-Boudreau and Conklin (1984)
32	*Panulirus homarus*	Growth and moulting	Effect of eyestalk ablation	Radhakrishnan and Vijayakumaran (1984)
33	*Homarus americanus*	Growth and energy utilization	Effect of eyestalk ablation, diets and environment	Koshio (1985)
34	*Nephrops norvegicus*	Growth	Nil	Sarda (1985)

35	*Panulirus polyphagus*	Growth	Reared from puerulus to adult	Radhakrishnan and Devarajan (1986)
36	*Homarus americanus*	Growth and survival	Effect of dietary cadmium	Chou *et al.* (1987)
37	*Panulirus argus*	Growth	Effect of eyestalk ablation	Diaz-Iglesia *et al.* (1987)
38	*Panulirus polyphagus*	Growth	Pit culture in the intertidal zone	Sarvaiya (1987)
39	*Panulirus homarus*	Growth	In marine cages	Kuthalingam (1988)
40	*Homarus americanus*	Growth and survival	Early juvenile in a plankton diet	Barshaw (1989)
41	*Homarus americanus*	Growth	Using human growth hormone	Charmantier *et al.* (1989a)
42	*Homarus americanus*	Growth	Using human somatotropin	Charmantier *et al.* (1989b)
43	*Homarus americanus*	Growth, feed efficiency and survival	Effect of eyestalk ablation, temperature and salinity	Koshio *et al.* (1989)
44	*Homarus americanus*	Growth and survival	Effect of varying dietary energy levels in eyestalk ablated and normal lobsters	Koshio *et al.* (1990)
45	*Panulirus argus*	Growth, survival and feed intake	Effect of temperature in post larvae	Lellis and Russel (1990)
46	*Jasus edwardsii*	Growth	Effect of various factors in captivity	Manuel (1991)
47	*Jasus edwardsii*	Growth and survival	Nil	Rayns (1991)
48	*Jasus edwardsii*	Growth	Nil	Bunter and Westaway (1993)
49	*Panulirus homarus*	Growth	Effect of sex/or reproductive activity	Jong (1993)
50	*Panulirus versicolor*	Growth and moulting	Comparision betweeen normal and eyestalk ablated lobsters	CARI (1994)
51	*Panulirus polyphagus*	Growth and feeding	Pit culture in intertidal zone	Philipose (1994)
52	*Panulirus homarus*	Growth	Economic assessment	Rahman *et al.* (1994)

53	*Homarus americanus*	Growth and survival	Using warm water from power station	Sakurai *et al.* (1994)
54	*Panulirus versicolor*	Growth and moulting	From puerulus stage to juvenile stage	CARI (1995)
55	*Panulirus argus, P. laevicauda and P. echinatus*	Growth	In nearshore cages	Assad et al. (1996)
56	*Homarus gammarus*	Growth and survival	Under culture conditions	Carrasco and Barros (1996)
57	*Panulirus ornatus*	Growth and food conversion	Effect of eyestalk ablation in juveniles	Juinio-Menez and Ruinata (1996)
58	*Panulirus argus*	Growth	In portable sea enclosures	Lozano-Alvarez (1996)
59	*Panulirus cygnus*	Growth	Morphological changes in pueruli and juveniles	Abrunhosa and Kittaka (1997b)
60	*Homarus americanus*	Growth	In new-shell lobsters	Donahue *et al.* (1997)
61	*Jasus edwardsii*	Growth and mortality	3 size classes held for > one year	Hooker *et al.* (1997)
62	*Jasus edwardsii*	Growth and moulting	Effect of feed freshness	James and Tong (1997)
63	*Homarus americanus*	Growth, survival and moulting	Formulated diets in 13-14 stage lobster	Lim *et al.* (1997)
64	*Panulirus argus*	Growth and behaviour	Effect of predation risk	Lozano-Alvarez and Spanier (1997)
65	*Panulirus japonicus*	Growth and moulting	Effect of temperature on phyllosoma	Matsuda and Yamakawa (1997)
66	*Thenus orientalis*	Growth and moulting	Effect of photoperiod	Mikami and Greenwood (1997)
67	*Panulirus homarus*	Growth, feeding rate and moulting	Different size groups under mass rearing	Rahman *et al.* (1997)
68	*Homarus americanus*	Growth	Effect of dissolved oxygen	Bayer *et al.* (1998)
69	*Jasus edwardsii*	Growth	Opened vs unopened mussel as feed	James (1998)

70	*Homarus gammarus*	Growth and survival	Rearing in cages on the seabed	Uglem *et al.* (1998)
71	*Homarus americanus*	Growth	Effect of soybean-based diets	Donahue *et al.* (1999)
72	*Homarus gammarus*	Growth and survival	In laboratory and cage culture	Knudsen and Tveite (1999)
73	*Jasus edwardsii*	Growth and survival	Effect of light intensity and food density in stage I, III and V phyllosomas	Moss *et al.* (1999)
74	*Panulirus cygnus*	Growth	Comparision of natural and pelleted food	Tsvetnenko *et al.* (1999)
75	*Jasus edwardsii*	Growth and survival	Effect of diet, temperature and tank environment	Crear *et al.*, (2000)
76	*Jasus edwardsii*	Growth and survival	Effect of l-carnitine	Dias-Wanigasekera *et al.* (2000)
77	*Homarus americanus*	Growth and survival	Effect of soybean-based diets	Floreto *et al.* (2000a)
78	*Jasus lalandii*	Growth, moulting and food consumption	Effect of temperature	Hazeli *et al.* (2000)
79	*Jasus edwardsii*	Growth	Effect of stocking density and shelter	James and Tong (2000)
80	*Panulirus ornatus*	Growth and survival	Effect of stocking density	Jones (2000)
81	*Homarus gammarus*	Growth and survival	Effect of communal rearing with natural bottom substrate	Jorstad *et al.* (2000)
82	*Jasus edwardsii*	Growth, survival, feeding and metabolic activity	Effect of temperature	Thomas *et al.* (2000)
83	*Homarus americanus*	Growth	With pelleted and natural food	Floreto *et al.* (2001)
84	*Panulirus cygnus*	Growth and moulting	With pelleted and natural food	Glencross *et al.* (2001)
85	*Homarus gammarus*	Growth	Effect of feeding frequency	Mente *et al.* (2001)
86	*Panulirus homarus*	Growth and survival	Effect of stocking density	Babu *et al.* (2002)

Food consumption				
87	*Panulirus japonicus*	Feeding	Patterns of feeding	Kubo and Masuda (1964)
88	*Jasus lalandii*	Feeding activity	Fed on a mixed diet including fish	Paterson (1969)
89	*Homarus americanus*	Feeding behaviour	Effect of crude oil	Atema and Stein (1974)
90	*Homarus americanus*	Consumption	Effect of food density and water temperature	Carlberg and Van Olst (1976)
91	*Homarus gammarus*	Consumption	Nil	Branford (1979)
92	*Panulirus cygnus*	Feeding	Preference between live and stale food	Tamm (1980)
93	*Homarus americanus*	Consumption and growth	Effect of temperature, photoperiod and feeding schedule	Bordner and Conklin (1981)
94	*Homarus* sp.	Assimilation	In hybrid lobsters	Bordner *et al.* (1983)
95	*Panulirus homarus*	Food intake and conversion	Effect of eyestalk ablation	Vijayakumaran and Radhakrishnan (1984)
96	*Homarus americanus*	Digestability	An evaluation of gravimetric and inert marker	Leavitt (1985)
97	*Jasus lalandii*	Food intake, defaecation and absorption	Nil	Zoutendyk (1988a)
98	*Jasus lalandii*	Daily consumption rates	In males held in captivity for over 400 days	Zoutendyk (1988b)
99	*Homarus gammarus*	Digestion	In larvae	Kurmaly *et al.* (1990)
100	*Nephrops norvegicus*	Rate of digestion	Natural feeds	Sarda and Valladares (1990)
101	*Homarus americanus*	Digestability, O_2 consumption and ammonia excretion	Effect of eyestalk ablation and diets with varying energy levels	Koshio *et al.* (1992)
102	*Homarus gammarus*	Carbohydrate digestion	Nil	Glass and Stark (1996)
103	*Jasus edwardsii*	Feeding technique	Fed with cultured and wild mussels	James and Tong (1998)

104	*Jasus edwardsii*	Consumption rate, growth and survival	Effect of brine shrimp size on stages I, III and V phyllosoma larvae	Tong *et al.* (2000)
Excretion				
105	*Jasus edwardsii*	Nitrogen excretion	Role of antennal gland	Binns and Peterson (1969)
106	*Homarus gammarus*	Ammonia excretion and food consumption	In recirculation systems	Wickins (1985)
107	*Jasus lalandii*	Nitrogen excretion	Its contribution to the inshore Benguela System	Zoutendyk (1987)
108	*Panulirus argus*	Ammonia excretion and oxygen consumption	With respect to body weight	Diaz-Iglesia *et al.* (1996)
Respiration				
109	*Nephrops norvegicus*	Respiration	Nil	Bohn (1901)
110	*Homarus vulgaris*	O_2 uptake	Nil	Thomas (1954)
111	*Nephrops norvegicus*	Respiration	In muscle tissues	Mattisson (1959, 1961a, 1961b)
112	*Homarus americanus*	O_2 uptake	Nil	Mc Leese (1964)
113	*Panulirus interruptus*	Respiration	Effect of body weight, O_2 concentration, temperature and activity	Winget (1969)
114	*Nephrops norvegicus*	Respiration	Nil	Atkinson (1971)
115	*Panulirus argus* and *P. guttatus*	Respiration rate	Effect of body size, DO, salinity and temperature	Buesa (1979)
116	*Nephrops norvegicus*	O_2 uptake	Effect of moult cycle	Sarda (1980)
117	*Nephrops norvegicus*	O_2 uptake	Effect of moult cycle and body size	Alcaraz and Sarda (1981)
118	*Homarus gammarus*	O_2 uptake	In young lobsters	Hagerman (1982)
119	*Homarus americanus*	O_2 uptake	Effect of moulting	Penkoff and Thurberg (1982)

120	*Panulirus polyphagus*	Respiratory metabolism	Effect of salinity, temperature and O_2 partial pressure	Kasim (1986)
121	*Homarus americanus*	Oxygen uptake	Effect of handling	Winkler (1987)
122	*Jasus lalandii*	Metabolic rate	In different size groups	Zoutendyk (1989)
123	*Panulirus cygnus*	Metabolic rate	Effect of temperature and developmental stage	Lemmens (1994)
124	*Homarus gammarus*	Metabolic rate	Effect of simulated seasonal temperature changes	Tully *et al.* (2000)
Moulting				
125	*Panulirus japonicus*	Moult cycle	Hormonal regulation	Schawbe *et al.* (1952)
126	*Panulirus cygnus*	Moulting behaviour	Nil	Thomas (1966)
127	*Nephrops norvegicus*	Moulting	Nil	Figueirdo and Thomas (1967)
128	*Jasus lalandii*	Moulting	Nil	Paterson (1968)
129	*Homarus americanus*	Moulting	Nil	Aiken (1973)
130	*Homarus americanus*	Moulting	Nil	Aiken (1980)
131	*Homarus americanus*	Moulting frequency	Influence of behaviour	Cobb *et al.* (1982)
132	*Panulirus argus*	Moult cycle alterations	Effect of feed	Lipcius and Herrinkind (1982)
133	*Panulirus marginatus*	Moulting	Stages of moult cycle	Lyle and Mac Donald (1983)
134	*Jasus lalandii*	Moulting	Carbon and nitrogen loss	Zoutendyk (1988c)
135	*Thenus orientalis*	Moulting	In females	Rahman and Subramoniam (1989)
136	*Panulirus argus*	Moult cycle	Using an index of pleopod cuticular morphology	Turnbull (1989)
137	*Homarus gammarus*	Moulting	With natural food and compounded diets	Ali and Wickins (1994)

138	*Panulirus argus*	Moulting	Effects on DNA in the hepatopancreas	Altman *et al.* (1994)
139	*Jasus frontalis*	Moulting	Stages of moult cycle	Elorza and Dupre (1996)
140	*Panulirus homarus*	Moulting	Nil	Radhakrishnan and Vijayakumaran (1998)
141	*Homarus gammarus*	Moulting and growth	Postlarvae	Scovacricchi *et al.* (1999)
142	*Homarus americanus*	Moulting	Nil	Waddy and Aiken (1999)
143	*Jasus frontalis*	Moulting	Nil	Dupre (2000)
144	*Jasus lalandii*	Moult cycle	Using epidermal retraction and degree of setal development in the pleopods	Isaacs *et al.* (2000)
145	*Jasus edwardsii*	Moulting	Stages of moult cycle	Musgrove (2000)
146	*Metanephrops challengeri*	Moult cycle	With premoult cuticular folding as an index	Oliver and Cryer (2000)
147	*Panulirus japonicus*	Moulting	In the pueruli	Sekine *et al.* (2000)
148	*Panulirus homarus*	Moulting stages	Biochemical changes in heamolymph, hepatopancreas and muscle	Dharani *et al.* (2002)

Vijayakumaran, 1990). Barring Logan and Epifanio (1978), who have estimated all the parameters of the energy budget, the other workers have estimated one or the other parameter and calculated the remaining parameters; or have used the data collected from other sources (Table 5).

Table 5. List of important literature on the energy budget of lobsters

Sl. no.	Species	Location	Parameters studied						Remarks	Reference
			C	P	E	R	F	U		
1	*Homarus americanus*	St. Margarets Bay, Novascotia	#	#	*	@	$	*	Wild	Miller *et al.* (1971)
2	*Homarus americanus*	Not Available	@	@	@	@	@	@	From hatching to early juveniles	Logan and Epifanio (1978)
3	*Jasus lalandii*	Malgas Island	#	$	$	@	*	$	Wild	Barkai and Branch (1988)
4	*Panulirus homarus*	Chennai, India	@	@	@	#	@	@	Fed on mussel, clam, fish and mixed food	Radhakrishnan (1989)
5	*Panulirus homarus*	Chennai, India	@	@	@	#	@	@	Various size groups fed on clam	Vijayakumaran (1990)

@ = Estimated
# = Calculated
* = Not considered
$ = From other sources

C = Consumption
P = Growth
E = Exuvia
R = Metabolism
F = Faecal matter
U = Nitrogenous excretion

MATERIAL AND METHODS

3. MATERIAL AND METHODS

3.1 Collection of Animals and Experimental Protocol

3.1.1 Seasonal variation in the landings and proximate composition

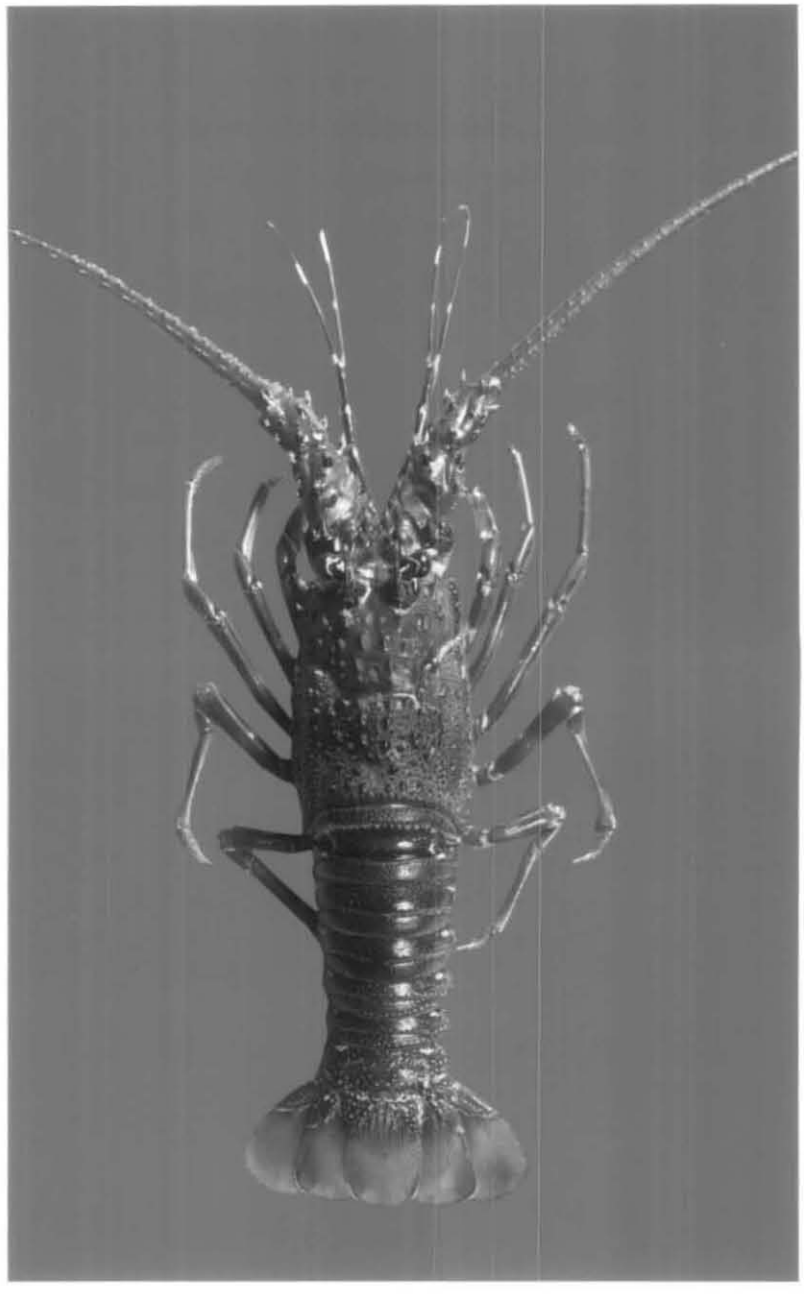
Data on the spiny lobster landings at the Chennai Fisheries Harbour (lat. 13° 05' N, long. 80° 11' E) were collected once in a week (1 st, 8 th, 15 th and 22 nd day of every month) from February 1999 to January 2000. Observations were made during hours of peak landings, *i. e.* between 6 am and 6 pm. The data were weighted for monthly values by using the following raising factor (Rf):

$$Rf = \frac{\text{Number of days of observation in a month}}{\text{Number of fishing days in that month}}$$

In addition to the collection of data on the landings, the species composition of the lobsters in the landings was also recorded. Since all the landed lobsters were exported, the details regarding the landings were ascertained from the lobster holding sheds owned by the exporters in the landing centre.

For studying the variations in biochemical constituents, samples of live *Panulirus homarus* (Plate 1) were collected once in a fortnight on the 1st and 15th of every month and transported to the laboratory with least stress and transferred into aquaria containing well aerated, filtered seawater. They were sacrificed within 24 hours for various analyses. During each sampling, 8 juvenile (body weight: 50-100g) and 8 maturing lobsters (body weight: 150-200g) were collected. In the 150-200g size group, the gonads of more than 50% of the lobsters were in mature condition and in the 50-100g size group, the gonads were immature. To overcome the sex related differences in the biochemical composition, equal number (4 numbers each) of males and females were used. Only healthy lobsters in the intermoult stage (C) were collected for analysis. Since changes in the biochemical composition are associated

Plate 1



Dorsal view of the spiny lobster *Panulirus homarus*

with the moult cycle, care was taken to collect lobsters in the same moult stage; the intermoult is the logical choice, since it is by far the longest and most stable stage.

3.1.2 Effect of starvation

For the experiment on starvation, *P. homarus* were collected from gillnet landings at Kovalam landing centre, near Chennai.They were acclimatized in the Kovalam Field Centre of CMFRI for ten days in filtered seawater of 32 ± 0.8 ppt salinity in a well aerated fibreglass tank (capacity: 1 ton). The lobsters were fed *ad libitum* with live clam, *Donax* spp. During the acclimation period, 50 % of water was changed daily. For the experiments, stage C (intermoult) lobsters were used.

For the experiment on starvation, 48 healthy lobsters were selected from the stock tank and reared individually in blue circular plastic aquaria (capacity: 20 l). The mean weight of the experimental lobsters was 103.9 ± 16.3 g and the mean carapace length was 48.0 ± 1.7 mm. The lobsters were divided into two groups of control and bilaterally eyestalk ablated lobsters of 24 each. At the commencement of the experiment, 4 individuals (2 males and 2 females) were sacrificed to estimate the proximate composition and energy content. The lobsters were not fed during the entire experiment. Four control lobsters (two males and two females) were sacrificed in the I, II, III, VI and IX week after initiation of starvation and the remaining four lobsters were allowed to die of starvation. Four ablated lobsters (two males and two females) were sacrificed in the I, II, III and VI week after initiation of starvation. The remaining animals were maintained until death.

3.1.3 Effect of different food on food utilization

For the experiment on energetics, healthy individuals of *P. homarus* were collected and maintained in the laboratory as mentioned in the section 3.1.2. For the experiment, a completely randomized design in a 4 x 4 factorial was followed. Each dietary treatment was carried out with a single animal with four replicates. For the feeding experiment, 16

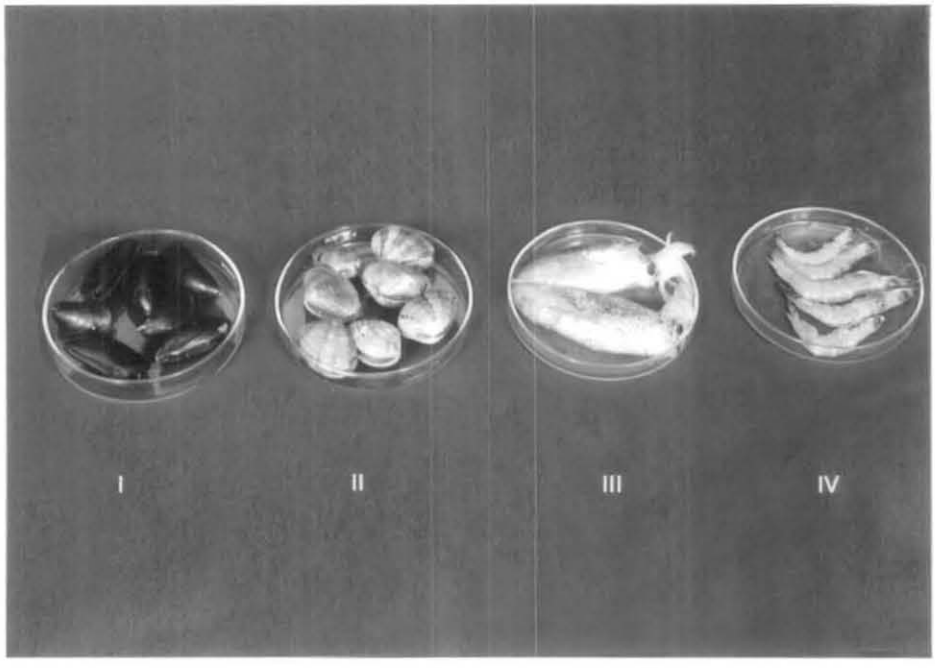
(8 male and 8 female) healthy and natural coloured lobsters in intermoult stage (C stage) were selected from the stock tank. The mean weight of the experimental lobsters was 95.1 ± 10.1 g and the mean carapace length was 45.2 ± 1.5 mm. The experimental lobsters were reared individually in blue coloured circular plastic aquaria (capacity 50 l). Stones were provided in the aquaria for lobster shelter. Among the 16 lobsters, four groups of 4 each (2 males + 2 females) were formed to test the effect of 4 different feeds on the food utilization parameters. For providing constant aeration, air pumps with air stone were connected to all the aquaria from an air compressor.

The natural feeds used in the experiment were shrimp (*Penaeus indicus*), squid (*Loligo duvauceli*), clam (*Paphia malabarica)* and mussel (*Perna viridis*) (Plate 2a). All the feed materials were procured from the market, cleaned and frozen in a deep freezer at -20°C. The maximum storage period of the feed was 10 days. The shrimp was offered as small pieces after removing the head; the squid was offered as small pieces after removing the intestine and suckers; the clam and mussel were offered after removing the shells (Plate 2b).

The lobsters were weighed once in a fortnight to determine the growth. During the experimental period, all the lobsters moulted twice and reached the intermoult stage. The experiment was conducted for 105 days.

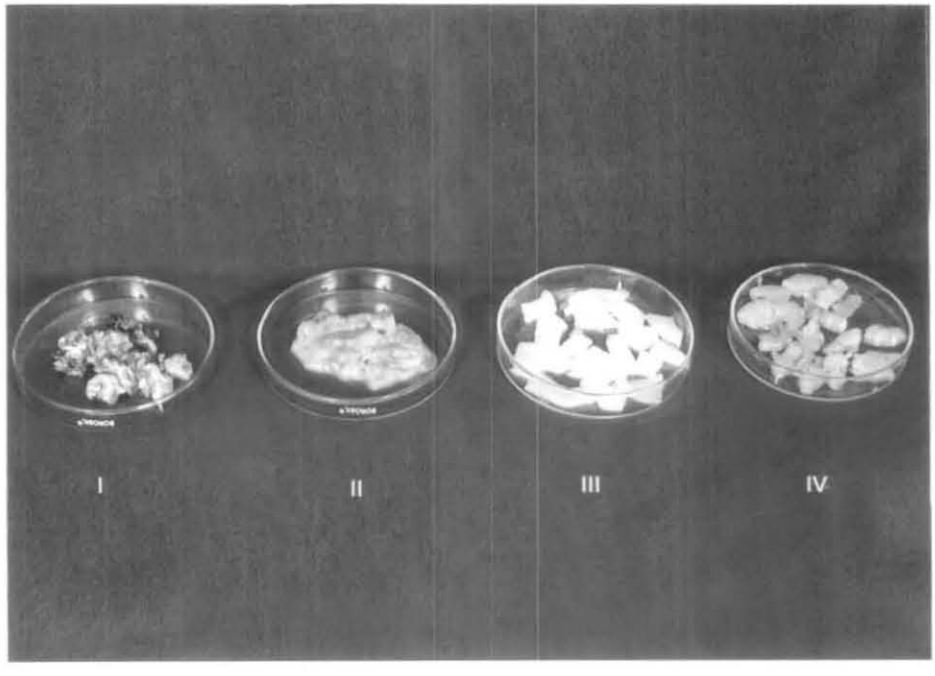
At the commencement of the experiment, 4 individuals (2 males and 2 females) were sacrificed to estimate the proximate composition and energy content. At the completion of the experiment, the lobsters were weighed and frozen. The tissues (muscle, hepatopancreas and exoskeleton) were dissected out and dried at 100 ± 5 °C to determine the water content and then powdered and stored in a dessicator for further biochemical and calorific determinations.

Plate 2



2a. Food materials offered to *P. homarus* in whole form

I. *Perna viridis* II. *Paphia malabarica* III. *Loligo duvauceli* IV. *Penaeus indicus*



2b. Food materials of *P.homarus* in the form in which it was offered

I. *Perna viridis* II. *Paphia malabarica* III. *Loligo duvauceli* IV. *Penaeus indicus*

3.2 Length and weight

The size of the spiny lobster *P. homarus* was recorded by measuring the carapace length (CL) to 0.1 mm accuracy along the mid dorsal line from the ridge behind the eyes (between the rostral horns) to the posterior margin of the carapace. This was used as the standard length (Berry, 1971) in the present study. The total length is laborious to measure and the accuracy is limited by the distortion of the abdomen. The carapace, being rigid, can be measured accurately with a vernier caliper. The live body weight was measured after removing the adhering free water as described by Chittleborough (1975). All the weighings on the tissues such as muscle, hepatopancreas and exoskeleton; feed, faecal matter and moult were made in an electrical balance to an accuracy of 1 mg; and the live body weight was determined by using a top pan balance to an accuracy of 0.1g.

3.3 Moult Stage

The moult stages were determined as described by Radhakrishnan (1989), in which the moult stages were differentiated by the morphological changes of the setae in the developing pleopods. Only lobsters in the intermoult stage (C stage) were used for all the experiments, since changes in the biochemical composition were associated with the moult cycle. The intermoult stage was the logical choice for the experiments, since it is by far the longest and most stable stage.

3.4 Proximate Composition

The water content was determined by keeping the tissues in a hot air oven at 100 $\pm$ 5 °C, until the tissues attained constant weight. The difference between the wet and dry weights was taken as moisture content and expressed as percentage of wet weight. Protein content in the tissues was determined by biuret method, using bovine serum albumin as standard, as suggested by Gornall *et al.* (1949). Total lipid was estimated by gravimetric method as suggested by Floch *et al.* (1957)

and modified by Linford (1965). Carbohydrate was estimated by phenol sulphuric acid method of Dubious *et al.* (1956). Ash content was determined from the residue remaining after incineration of samples at 550°C in a muffle furnace.

3.5 Bomb Calorimetry

Calorimetric determinations were made with an Advance isothermal bomb calorimeter. Benzoic acid was used as the standard. The bomb calorimeter was standardized daily before commencement of energy determination. The dry powdered samples kept in the dessicator for biochemical analyses were used for calorimetry. The powdered samples, with the help of a hand press, were made into pellets before energy determination. Since the samples of faeces were inadequate for energy determination, the samples were substituted with known quantity of standard benzoic acid.

3.6 Hepatosomatic and Muscle Index

Dry hepatosomatic index (HSI_d) was determined by using the following equation:

$$HSI_d\ (\%) = \frac{\text{dry weight (g) of hepatopancreas}}{\text{dry weight (g) of whole animal}} \times 100$$

The proportion of the wet tail muscle to the total body weight (wet Tail Muscle Index: TMI_w) was determined by using the following equation:

$$TMI_w = \frac{\text{wet weight (g) of tail muscle}}{\text{wet weight (g) of whole animal}} \times 100$$

The dry Tail Muscle Index (TMI_d) was calculated by using the following equation:

$$TMI_d = \frac{\text{dry weight (g) tail muscle}}{\text{dry weight (g) of whole animal}} \times 100$$

The tail muscle refers to the abdominal muscle portion of the lobster excluding the exoskeleton.

3.7 Eyestalk Ablation

Eyestalk ablation or destalking was performed by cutting both the eyestalks (bilateral ablation) at their base with a fine pair of dissecting scissors. The wound was closed by keeping the finger pressed on it for a minute. The stress was minimised by removing only one eyestalk in a day and the other was removed the following day. At no instance, the wound got infected. No mortality occurred due to the ablation stress.

3.8 Water Quality Parameters

During the experimental period, the water quality parameters such as temperature (centigrade thermometer), pH (digital pH meter), salinity (refractometer) and dissolved oxygen (Wrinkler's method: Strickland and Parsons (1972) were monitored every alternative day. The range of values are given in Table 6.

3.9 Protein-Energy Ratio

The protein-energy ratio was calculated as follows:

$$P:E = \frac{\text{g protein/g}}{\text{k cal/g}}$$

Table 6. Water quality parameters observed during the experiments

Experiment	Parameter	Range	Mean ± sd
Effect of starvation	Temperature (^{0}C)	25.2-27.8	26.5 ± 1.3
	pH	7.6-8.1	7.9 ± 0.3
	Salinity (ppt)	29.8-32.7	31.6 ± 1.6
	Dissolved oxygen (mg/lit)	4.2-4.7	4.5 ± 0.3
Effect of different food on food utilization	Temperature (^{0}C)	24.5-27.4	26.1 ± 1.5
	pH	7.7-8.2	8.0 ± 0.3
	Salinity (ppt)	31.0-33.9	32.4 ± 1.5
	Dissolved oxygen (mg/lit)	4.1-4.5	4.3 ± 0.2

3.10 Food Utilization Parameters

The bioenergetic parameters were calculated following the International Biological Programme (IBP) formula of Petrusewicz and MacFadyen (1970). The energy equation may be expressed as,

$$C = (P + E) + R + F + U$$

where, C = food consumed, P = growth, E = moult, R = the material lost as heat due to metabolism, F = faecal loss, and U = the nitrogenous excretory products.

Since the lobsters used in this study were sexually immature, caloric utilization in gamate production was not included in the energy budget.

3.10.1 Estimation of consumption (C)

The spiny lobsters feed mostly at night. Hence, pre-weighed food was provided to *P. homarus* at 1700 hrs daily and the unconsumed food was removed at 0800 hrs the following day. The frozen food was thawed, cleaned, cut into small pieces and weighed before feeding. The unconsumed food was siphoned carefully into a bolting silk, washed with distilled water, blotted dry and transferred to pre-weighed petriplates and dried at 100 $\pm$ 5 °C in an oven. Food consumption was estimated by subtracting the dry weight of the uneaten food from the dry weight of the food offered and the values were then converted into joules. The feeding rate is calculated as follows:

$$\text{Feeding rate (j/g/d)} = \frac{\text{Food energy consumed (C)}}{\text{Live mid-body weight of the lobster (g)} \times \text{day}}$$

$$\text{Live mid-body weight (g)} = \frac{W_0\,(g) + W_t\,(g)}{2}$$

where, W_0 = the initial live body weight; and W_t = live body weight at the end of the experiment

3.10.2 Estimation of faeces (F)

The faecal matter of *P. homarus* is in the form of ribbon strips, which settle at the bottom of the aquarium. The faeces were collected daily by siphoning into a bolting silk, rinsed with distilled water and dried in an oven at 100 ± 5 °C. Aeration was stopped while collecting the faeces. The faeces of the lobsters receiving the same food were pooled and the energy equivalent determined.

3.10.3 Estimation of nitrogen excretion (U)

In the crustaceans, ammonia forms more than 80% of the nitrogenous excretory products (Pandian, 1975). The excretion of ammonia by *P. homarus* was determined at biweekly intervals using phenol hypochlorite method of Solorzano (1969). For the estimation of ammonia excretion, two methods were followed. In the first method, the 4 different feeds were kept separately (without the lobster) in aquaria and the ammonia released by the feed in 24-hour duration was estimated. The quantity of ammonia in these aquaria was subtracted from the ammonia released in the experimental aquaria, 24 hours after feeding. Initial concentration of ammonia in the experimental aquaria was also determined and taken into consideration. In the second method, the ammonia excretion was estimated by determining the quantity of ammonia produced in the aquaria with filtered seawater to which the experimental lobsters were transferred immediately after feeding. The initial ammonia content in the water was determined prior to the introduction of the lobsters. Ammonia was determined 24 hours after the introduction of the lobster. The difference in the values of ammonia production between the two methods was negligible. For calculating the energy equivalent of ammonia loss, the value (1 mg ammonia = 20.5 j) reported by Brafield (1985) was applied.

3.10.4 Estimation of assimilation (A_e)

Assimilation (A_e) was calculated by subtracting the energy lost through faecal production (F) and nitrogen excretion (U) from the total energy consumed (C). The rate and efficiency of assimilation is calculated as follows:

$$\text{Assimilation rate (j/g/d)} = \frac{\text{Food energy assimilated (Ae)*}}{\text{Live mid-body weight of the lobster (g) x day}}$$

*Ae = C- (F+U)

$$\text{Assimilation efficiency (\%)} = \frac{\text{Food energy assimilated}}{\text{Food energy consumed}} \times 100$$

3.10.5 Estimation of growth (P & E)

Growth (P) was calculated by subtracting the initial dry weight / energy content of the animal from the final dry weight / energy content. To estimate the dry weight and energy content of the lobsters at the commencement of the experiment, the 'Sacrifice Method' of Maynard and Loosli (1962) was followed. A group of five animals of similar body weight and moult stage was used as control for determining the initial water and energy contents.

Since moult (E) too form a part of the converted energy in the crustaceans, the energy content of the moult was also considered to calculate the energy budget. The rate and efficiency of conversion is calculated as follows:

$$\text{Conversion rate (j/g/d)} = \frac{\text{Food energy converted (P+E)}}{\text{Live mid-body weight of the lobster (g) x day}}$$

$$\text{Gross conversion efficiency } (K_1)\ (\%) = \frac{\text{Food energy converted}}{\text{Food energy consumed}} \times 100$$

$$\text{Net conversion efficiency } (K_2)\ (\%) = \frac{\text{Food energy converted}}{\text{Food energy assimilated}} \times 100$$

$$\text{Food Conversion Ratio (FCR)} = \frac{\text{Food consumed (dry)}}{\text{Live weight gain}}$$

$$\text{Average daily wet weight gain (mg/day)} = \frac{\text{Final wet weight (mg) - Initial wet weight (mg/day)}}{\text{Experimental duration (days)}}$$

3.10.6 Estimation of metabolism (R)

Metabolism was calculated from the formula of energy budget. It includes the energy demands of metabolic maintenance and behavioural activities. Metabolic rate in the form of oxygen consumption was calculated by considering 20.098 j as the oxycaloric coefficient of one ml O_2 consumed (Engelman, 1966). The metabolic rate is calculated as follows:

Metabolic rate (j/g/d) = Assimilation rate - conversion rate

$$\text{Metabolic rate (ml } O_2\text{/g/hr)} = \frac{\text{Metabolic rate (j/g live mid-body weight/ day)}}{20.098 \times 24}$$

Table 8. Species composition (%) of spiny lobster landings at Chennai Fisheries Harbour between February 1999 and January 2000

Month & Year	*Panulirus homarus*	*Panulirus polyphagus*	*Panulirus ornatus*	*Panulirus versicolor*
February, 1999	47.2	48.5	4.3	0.0
March, 1999	50.0	50.0	0.0	0.0
April, 1999	100.0	0.0	0.0	0.0
May, 1999	21.2	10.6	57.6	10.6
June, 1999	61.0	24.2	12.7	2.1
July, 1999	82.8	12.6	1.7	2.9
August, 1999	81.6	3.6	11.6	3.2
September, 1999	83.8	11.2	5.0	0.0
October, 1999	62.1	29.2	5.4	3.3
November, 1999	100.0	0.0	0.0	0.0
December, 1999	82.7	12.1	0.0	5.2
January, 2000	98.6	1.4	0.0	0.0

Fig. 1. Composition of different species to the total lobster landings at Chennai Fisheries Harbour between February 1999 and January 2000

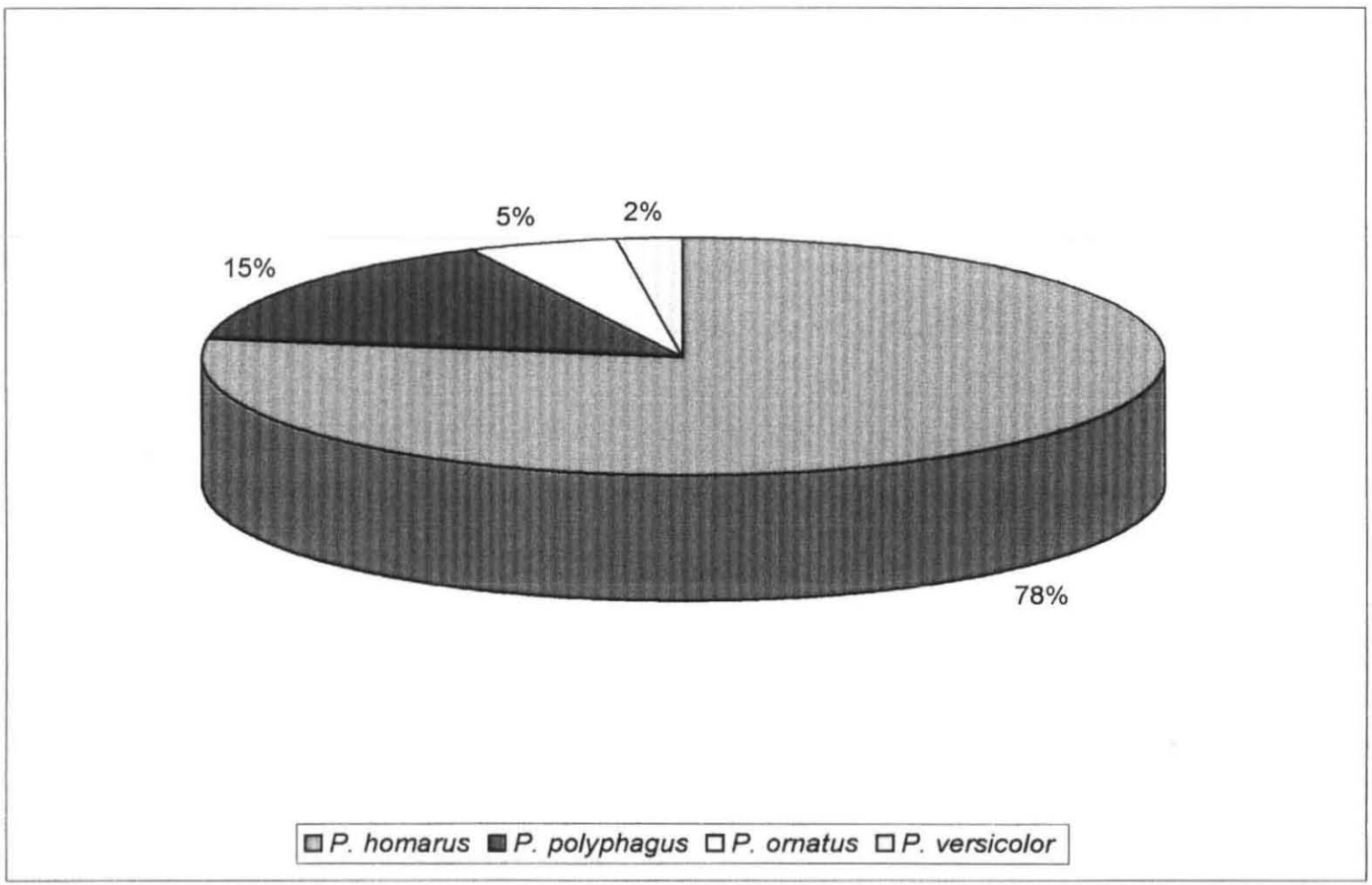


Table 7. Spiny lobsters landed (kg) at Chennai Fisheries Harbour

Month & Year	*Panulirus homarus*	*Panulirus polyphagus*	*Panulirus ornatus*	*Panulirus versicolor*	Total
February 1999	110	113	10	0	233
March 1999	98	98	0	0	196
April 1999	18	0	0	0	18
May 1999	14	7	38	7	66
June 1999	293	116	61	10	480
July 1999	659	100	14	23	796
August 1999	537	24	76	21	658
September 1999	615	82	37	0	734
October 1999	450	212	39	24	725
November 1999	506	0	0	0	506
December 1999	573	84	0	36	693
January 2000	421	6	0	0	427
February 1999 - January 2000	4294	842	275	121	5532

4. RESULTS

4.1 Seasonal Variation in the landings and proximate composition

4.1.1 Monthwise lobster landings at Chennai

The spiny lobsters were landed by bottomset gill nets and trawls at Chennai Fisheries Harbour. The estimated total landings were 5,532 kg during the study period (February 1999 to January 2000) (Table 7). The highest landings (796 kg) were observed in July 1999, and the lowest (18 kg) in April 1999. The fishing activity was very low off Chennai in April and May due to poor catches from the fishing grounds. Four species of spiny lobsters, *viz.*, *Panulirus homarus*, *P. polyphagus*, *P. versicolor* and *P. ornatus* contributed to the spiny lobster landings. Among the four species, the landings of *P. homarus* were maximum (4294 kg). *P. homarus* contributed 77.6 % to the total lobster catch (Fig. 1). The contribution of other species is as follows: *P. polyphagus* - 842 kg (15.2 %); *P. ornatus* - 275 kg (5.0%); and *P. versicolor* - 121 kg (2.2%). *P. homarus* was the major contributor to the lobster landings along the Chennai coast for 10 months during the study period. It contributed 100% to the lobster landings during April and November 1999 (Table 8).

4.1.2 Production of tail muscle, nutrients and calories through lobster fishery at Chennai

The composition of tail muscle ranged between 28.5 $\pm$ 0.2% (August, 1999) to 29.4 $\pm$ 0.2% (February and September, 1999) of the total wet weight of *P. homarus* (Fig. 2) with an average of 28.9 $\pm$ 0.3%. Maximum tail muscle (188.9 kg) from the fishery was available in July 1999 (Fig. 3), since the maximum landings were in that month. The quantity of tail muscle available was the lowest (4.1 kg) in May 1999. The annual production of tail muscle of *P. homarus* amounted to 1241.1 kg, consisting of 242.3 kg protein, 32.2 kg lipid, 5.0 kg carbohydrate and 6.3 x 10^6 kj energy (Table 9). The availability of tail muscle (121.0 to 188.9 kg/month; Fig. 3); protein (23.6 to 36.9 kg/month; Fig. 4); lipid (3.1 to 4.9

RESULTS

3.11 Statistical Analysis

The data were analysed using the statistical methods such as mean and standard deviation, Student's t test, and one way analysis of variance (ANOVA) and analysis of covariance (ANOCOVA). Percentage data was Arc Sin transformed prior to analysis. All the calculations were made following Snedecor and Cochran (1967). The different statistical methods applied in each chapter for interpreting the results obtained on specific parameters is given below:

Statistical test	Chapter		
	Seasonal variation in the landings and proximate composition	Effect of starvation	Effect of different food on food utilization
Student's t test	Comparison of dry tail muscle index and dry hepatosomatic index, proximate composition and energy content, between juveniles and maturing lobsters and between different tissues	Difference in survival period between control and ablated lobsters	Comparison of biochemical composition and energy contents in food materials; various tissues of lobsters and food utilization parameters
ANOVA	Comparison of fortnightly variations in dry tail muscle index and hepatosomatic index, proximate composition and energy content of different tissues, of juvenile and maturing lobsters	Effect of starvation on proximate composition, energy content and protein-energy ratio in various tissues of control and ablated lobsters	Nil
ANOCOVA	Nil	Comparison between control and ablated lobsters on the effect of starvation on proximate composition, energy content and protein-energy ratio in different tissues	Nil

Fig. 2 Composition (%) of tail muscle in the wet weight of *P. homarus* landed between February 1999 and January 2000 at Chennai Fisheries Harbour

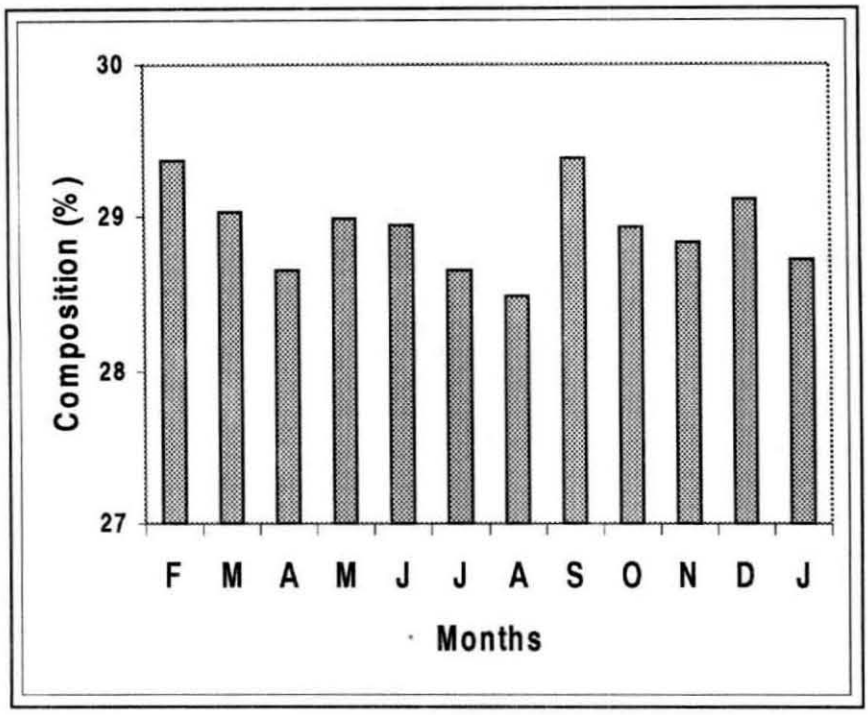


Fig. 3 Tail muscle production through *P. homarus* landings at Chennai Fisheries Harbour Between February 1999 and January 2000

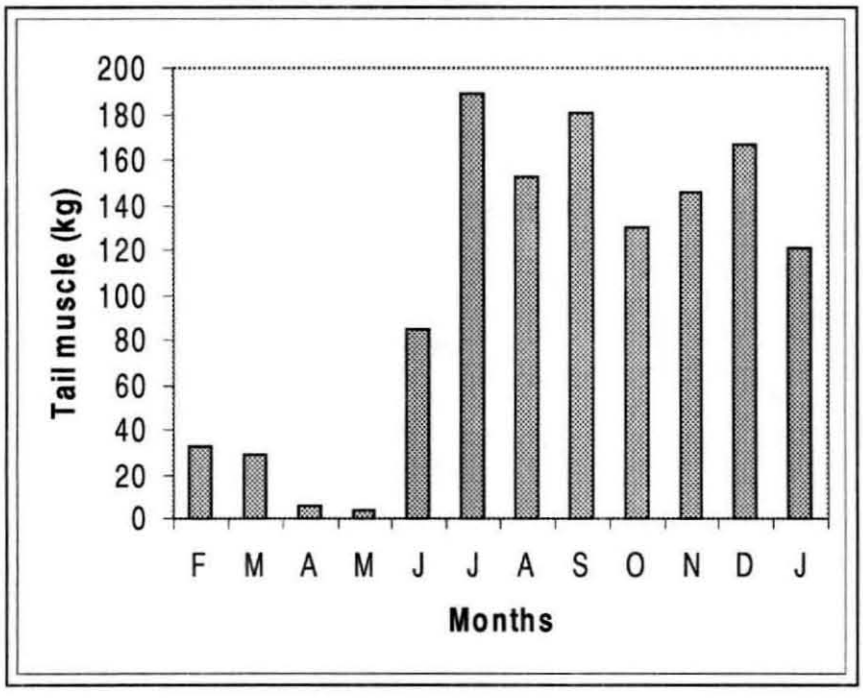


Fig. 4 Protein production through *P. homarus* landings at Chennai Fisheries Harbour between February 1999 and January 2000

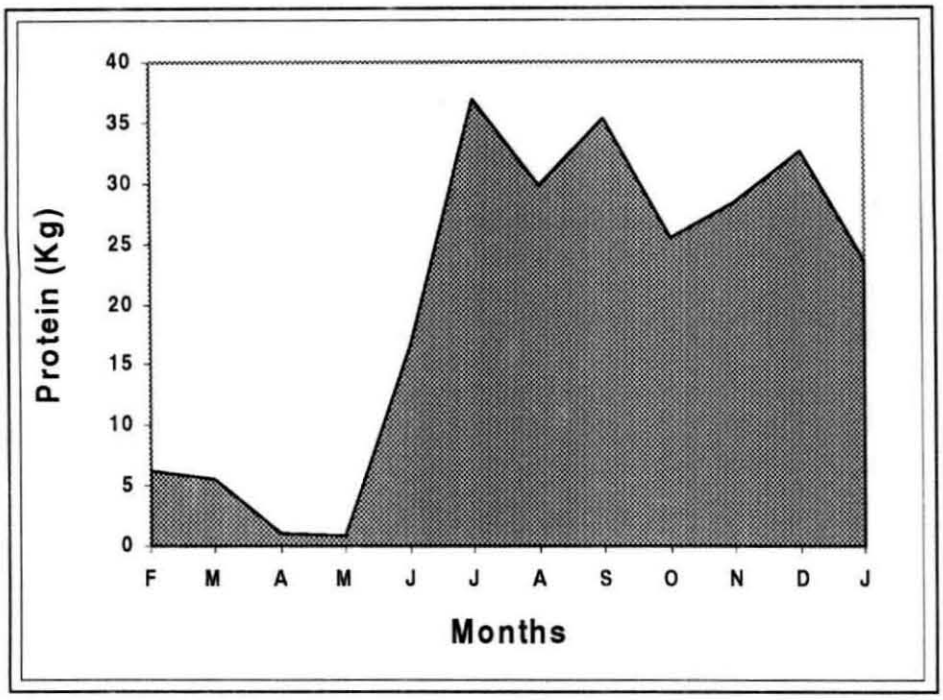
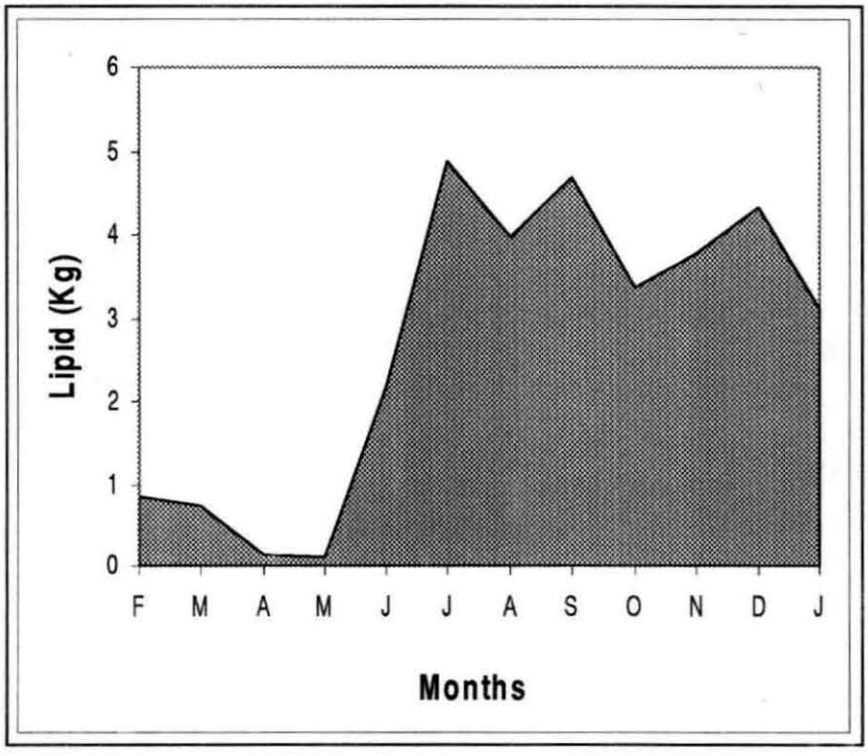


Fig. 5 Lipid production through *P. homarus* landings at Chennai Fisheries Harbour between February 1999 and January 2000



kg/month; Fig. 5); carbohydrate (0.5 to 0.8 kg/month; Fig. 6); and energy (0.6×10^6 to 1.0×10^6 kj/month; Fig. 7) was high during July, 1999 to January, 2000, which is in correspondence with the good landings recorded during that period (Table 7).

For estimating the total amount of nutrients produced through landings of all the spiny lobsters at Chennai, the estimated values on the proportion of tail muscle and the protein, lipid, carbohydrate and energy contents in the tail muscle of *P. homarus* were applied on the landings of the other three species of spiny lobsters. The annual tail muscle production (wet weight) of the spiny lobsters thus calculated was 1599.3 kg (Table 9) and the nutrient production (dry weight) was as follows: protein - 312.3 kg, lipid - 41.5 kg and carbohydrate - 6.4 kg. The annual energy production through the lobster fishery was 8.1×10^6 kj.

4.1.3 Proportion of weight of tail muscle and hepatopancreas in the total weight of lobster

4.1.3.1 Tail muscle

The proportion of dry weight of tail muscle to the dry weight of the lobster (TMI_d) ranged from 22.1 $\pm$ 0.4% to 23.6 $\pm$ 1.1% with an average of 22.8 $\pm$ 0.5% (Table 10) in the juveniles and between 22.5 $\pm$ 0.3% to 23.6 $\pm$ 0.7% with an average of 22.9 $\pm$ 0.3% (Table 10) in the maturing lobster. The mean values between the juvenile and maturing lobsters were not significantly different ($t = 0.80$; $p > 0.05$). The average TMId for both the size groups ranged from 22.41% (II fortnight of August) to 23.41% (II fortnight of September). The fortnightly fluctuations did not follow any specific trend (Fig. 8a); the ANOVA indicated that the difference between the fortnightly samples were not significantly different ($f= 0.79$; $p > 0.05$) (Appendix 1a).

Fig. 6 Carbohydrate production through *P. homarus* landings at Chennai Fisheries Harbour between February 1999 and January 2000

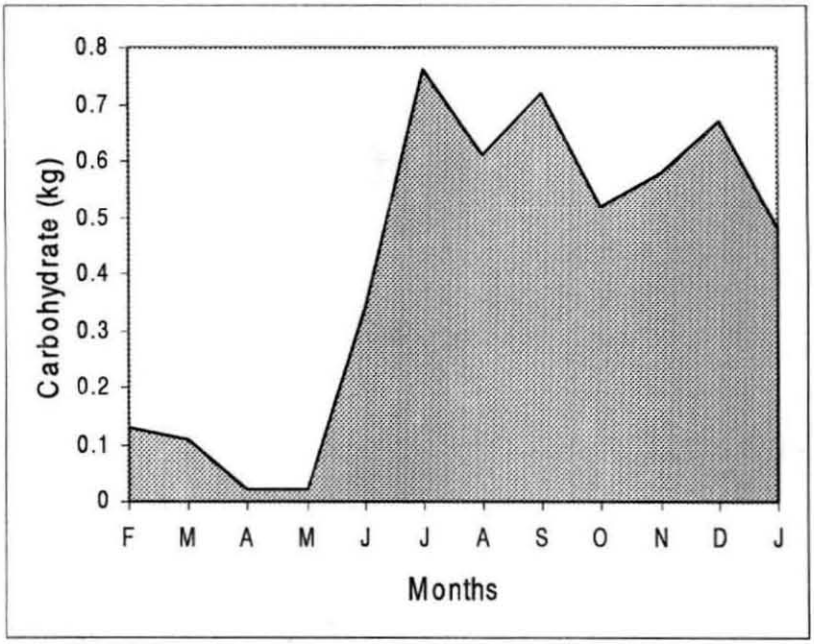


Fig. 7 Energy production through *P. homarus* landings at Chennai Fisheries Fisheries Harbour between February 1999 and January, 20000

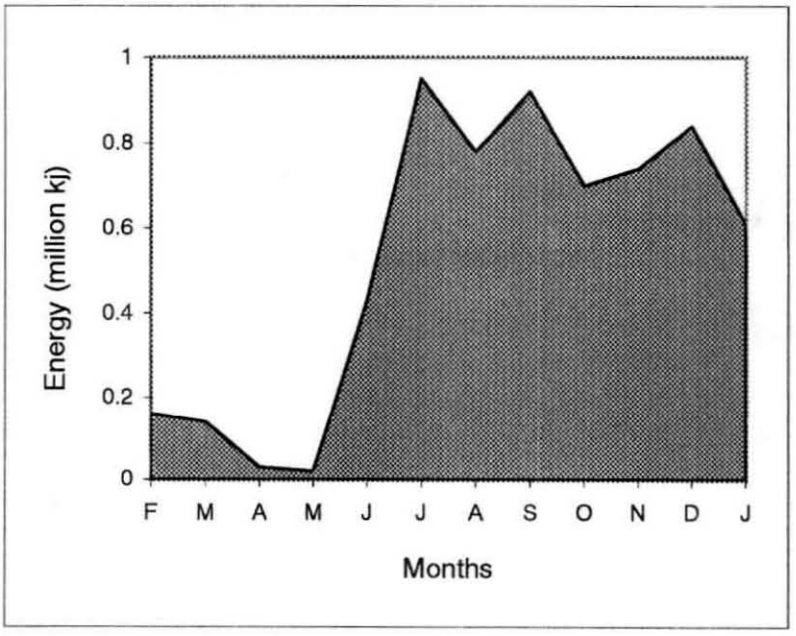


Table 9. Production of tail muscle, nutrients and energy through lobster fishery at Chennai during February 1999 - January 2000

Species	Wet weight of tail muscle (kg)	Protein (kg)	Lipid (kg)	Carbohy drate (kg)	Energy (kj)
P. homarus	1241.1	242.3	32.2	5.0	6.3×10^6
P. polyphagus *P. ornatus* *P. versicolor*	358.2	70.0	9.3	1.4	1.8×10^6
Total	1599.3	312.3	41.5	6.4	8.1×10^6

Table 10. Contribution of the tail muscle and hepatopancreas (% dry weight) in the total (dry) weight of *P. homarus* during February 1999 to January 2000

Maturity stage	Tail muscle	Hepatopancreas
Juvenile	22.76 ± 0.45	4.74 ± 0.08
Maturing	22.85 ± 0.30	4.67 ± 0.07
Juvenile + Maturing	22.80 ± 0.37	4.71 ± 0.08

Fig. 8 Proportion of the weight of tail muscle (8a) and hepatopancreas (8b) in the total weight of *P. homarus*; the vertical lines indicate standard deviation

Fig 8a

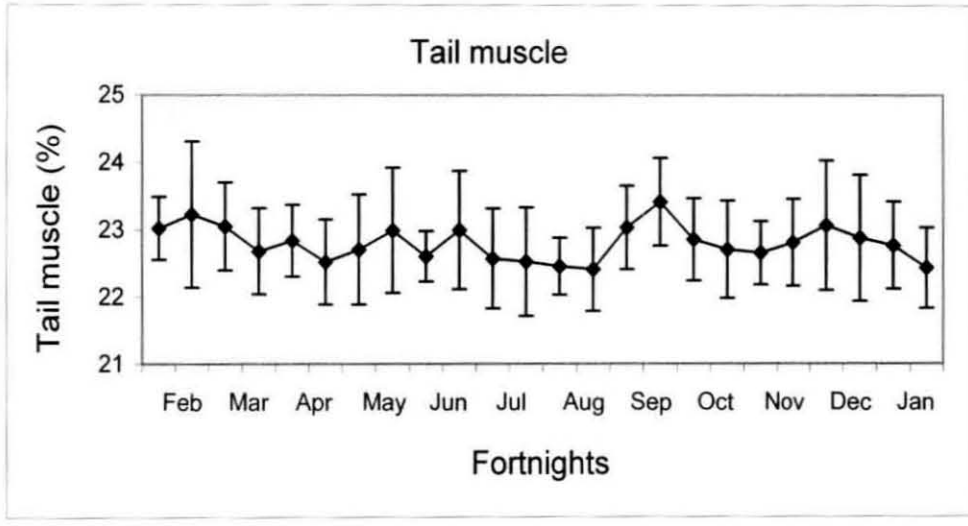
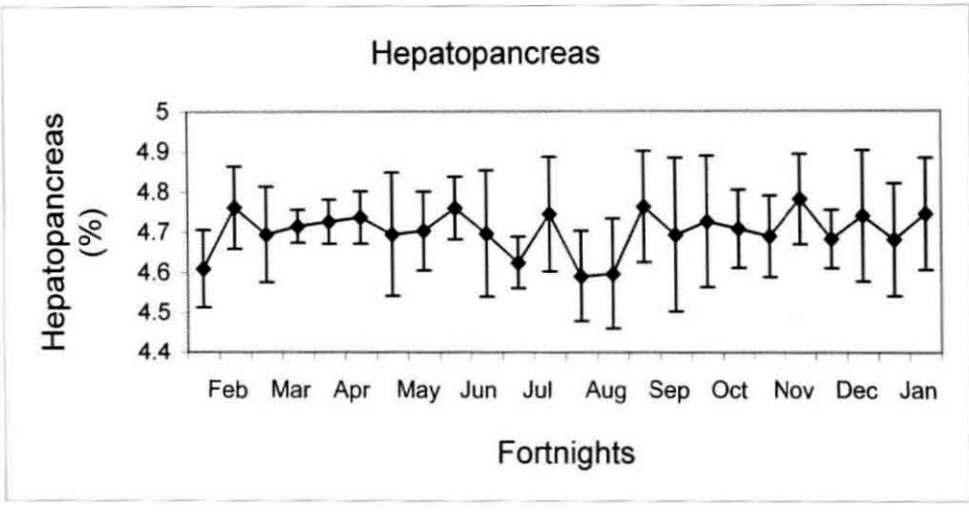


Fig. 8b



4.1.3.2 Hepatopancreas

The proportion of dry weight of the hepatopancreas to the total dry weight of the lobster (HSI_d) ranged from 4.6 ± 0.2% to 4.9 ± 0.1% with an average of 4.74 ± 0.08 (Table 10) in the juveniles and from 4.6 ± 0.1% to 4.8 ± 0.1% with an average of 4.67 ± 0.07% in the maturing lobsters (Table 10). The mean values between the juvenile and maturing lobster were significantly different ($t= 3.16$; $p< 0.01$). The average HSI_d in both the size groups ranged from 4.59% (I fortnight of August) to 4.78% (II fortnight of November). The fortnightly fluctuations did not follow any specific trend (Fig. 8b); the ANOVA indicated that the difference between the fortnightly variations were not significantly different ($f= 1.29$; $p > 0.05$) (Appendix 1b).

4.1.4 Comparison of proximate composition and energy content between juvenile and maturing lobsters

For the comparison of the proximate composition and energy content between the juvenile and maturing lobsters, the annual average values of each biochemical constituent were calculated.

4.1.4.1 Tail muscle

The annual mean water content in the tail muscle of the juvenile and maturing lobsters were 75.7 + 1.8 % and 76.1 + 2.2 % respectively; protein: 81.0 + 0.9% and 81.2 + 0.8%; lipid: 9.9 + 1.0 % and 9.7 + 1.1 %; carbohydrate: 1.7 + 0.3 % and 1.6 + 0.3 %; ash: 7.4 + 0.9 % and 7.5 + 0.8 %; and energy content: 20.9 + 0.5 kj/g and 21.1 + 0.5 kj/g between February 1999 and January 2000 (Table 11). No significant difference in any of the parameters was observed between the juvenile and maturing lobsters (Table 12).

4.1.4.2 Hepatopancreas

The mean water content in the hepatopancreas of the juvenile and maturing lobsters were 63.3 ± 1.8 % and 64.1 ± 1.9%; protein, 57.1 ± 0.7 % and 55.4 ± 1.0 %; lipid, 30.8 ± 1.6 % and 32.4 ± 1.9

Table 11. Average proximate composition (% dry weight) and energy content (kj/g) of the tail muscle, hepatopancreas and exoskeleton of juvenile and maturing lobsters during February 1999 to January 2000; ± represents standard deviation

TISSUE	MATURITY STAGE	WATER CONTENT	PROTEIN	LIPID	CARBOHY-DRATE	ASH	ENERGY
TAIL MUSCLE	JUVENILE	75.7 ± 1.8	81.0 ± 0.9	9.9 ± 1.0	1.7 ± 0.3	7.4 ± 0.9	20.9 ± 0.5
	MATURING	76.1 ± 2.2	81.2 ± 0.8	9.7 ± 1.1	1.6 ± 0.3	7.5 ± 0.8	21.1 ± 0.5
HEPATOPANCREAS	JUVENILE	63.3 ± 1.8	57.1 ± 0.7	30.8± 1.6	5.5 ± 0.7	6.6 ± 0.7	24.6 ± 0.7
	MATURING	64.1 ± 1.9	55.4 ± 1.0	32.4 ± 1.9	5.7 ± 0.6	6.5 ± 0.9	24.5 ± 0.8
EXOSKELETON	JUVENILE	38.4 ± 1.5	3.4 ± 0.3	1.1 ± 0.1	1.6 ± 0.1	93.9 ± 0.4	0.09 ± 0.02
	MATURING	37.5 ± 1.9	3.5 ± 0.4	0.9 ± 0.2	1.9 ± 0.2	93.7 ± 0.5	0.09 ± 0.01

Table 12. Results of the analysis of Student`s t test for the proximate composition (%dry weight) and energy content between juvenile and maturing *P. homarus*

TISSUE	Student`s t test	WATER	PROTEIN	LIPID	CARBOHYDRATE	ASH	ENERGY
TAIL MUSCLE	t value	0.68	0.80	0.65	1.13	0.40	1.36
	p value	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
HEPATOPANCREAS	t value	1.47	6.68	3.09	1.04	0.42	0.45
	p value	>0.05	<0.01	<0.01	>0.05	>0.05	>0.05
EXOSKELETON	t value	0.99	0.96	4.29	6.43	1.50	0.00
	p value	>0.05	>0.05	<0.01	<0.01	>0.05	>0.05

%; carbohydrate, 5.5 ± 0.7 % and 5.7 ± 0.6 %; ash, 6.6 ± 0.7 % and 6.5 ± 0.9 %; and energy content 24.6 ± 0.7 kj/g and 24.5 ± 0.8 kj/g respectively between February 1999 and January 2000 (Table 11). Barring protein (t = 6.68) and lipid (t = 3.09) no significant difference in the other parameters was observed between the juvenile and maturing lobsters (Table 12).

4.1.4.3 Exoskeleton

The mean water content in the exoskeleton of the juvenile and maturing lobsters were 38.0 ± 1.5 % and 37.5 ± 1.9 %; protein, 3.4 ± 0.3 % and 3.5 ± 0.4 %; lipid, 1.1 ± 0.1 % and 0.9 ± 0.2 %; carbohydrate, 1.6 ± 0.1 % and 1.9 ± 0.2 %; ash, 93.9 ± 0.4 % and 93.7 ± 0.5 %; and energy content, 0.09 ± 0.02 kj/g and 0.09 ± 0.01 respectively between February 1999 and January 2000 (Table 11). Barring lipid (t = 4.29) and carbohydrate (t = 6.43) no significant difference in the other parameters was observed between the juvenile and maturing lobsters (Table 12).

4.1.5 Fortnightly variations in proximate composition and energy content of different tissues of juvenile and maturing lobsters

4.1.5.1 Water content

The water content in the tail muscle of the juveniles ranged from 72.4% to 78.3% and that of the maturing lobsters from 71.2% to 79.5% in the fortnightly samples collected during February 1999 to January 2000. The average water content in both the size groups ranged from 73.5% (I fortnight of July) to 78.9% (I fortnight of February). The fortnightly fluctuations did not follow any specific trend (Fig. 9a); the ANOVA indicated that the difference between the fortnightly samples were not significantly different ($f = 0.99$; $p > 0.05$) (Appendix 2a).

The water content in the hepatopancreas of the juveniles ranged from 60.7% to 66.0% and that of the maturing lobsters from 59.9% to 66.4%. The average water content in both the size groups ranged from 61.2% (II fortnight of November) to 66.0% (I fortnight of

Fig. 9. Fortnightly variation in the water content of tail muscle, hepatopancreas and exoskeleton of *P. homarus* from February 1999 to January 2000

Fig. 9a

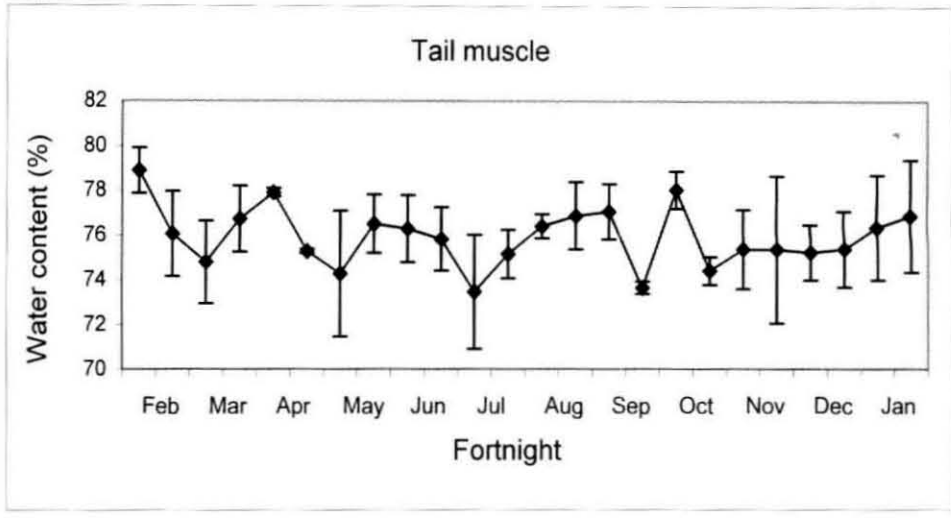


Fig. 9b

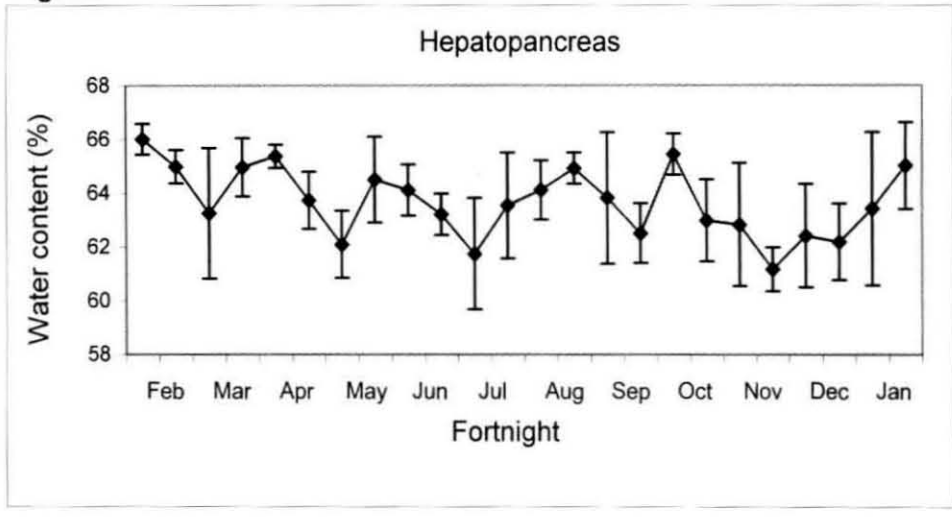
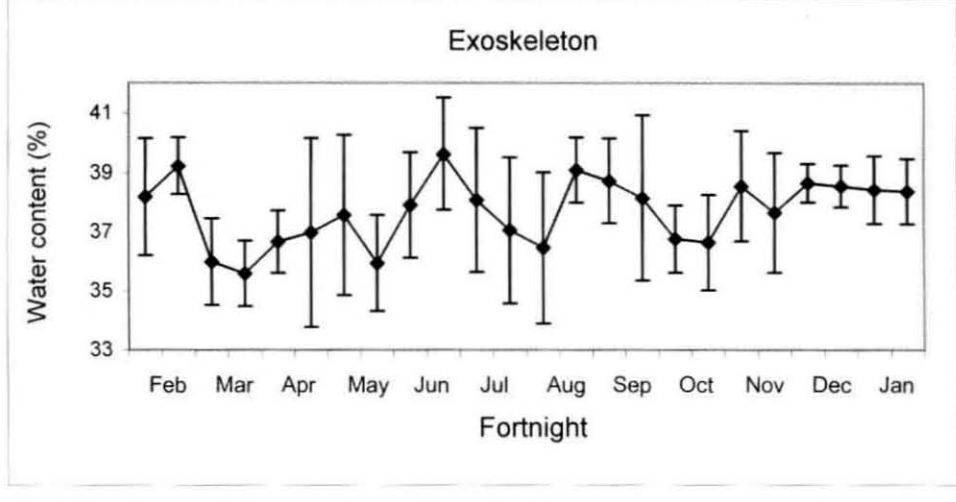


Fig. 9c



February). The fortnightly fluctuations did not follow any specific trend (Fig. 9b). However, the differences between the fortnightly samples were significantly different ($f = 4.29$; $p < 0.01$) (Appendix 2b).

The water content in the exoskeleton of the juveniles ranged from 35.4% to 39.9% and that of the maturing lobsters from 34.2% to 39.9%. The average water content in both the size groups ranged from 35.6% (II fortnight of March) to 39.6% (II fortnight of June). Eventhough a definite fortnightly trend was not evident (Fig. 9c), the variations were significantly different ($f = 2.25$; $p < 0.01$) (Appendix 2c).

4.1.5.2 Protein

The protein content in the tail muscle of the juveniles ranged from 79.6% to 82.8% and that of the maturing lobsters from 79.9% to 82.9% in the fortnightly samples collected during February 1999 to January 2000. The average protein content in both the size groups ranged from 80.3% (I fortnight of September and II fortnight of July) to 82.8% (II fortnight of March). The fortnightly variations did not follow any specific trend (Fig. 10a) and the variations were not significantly different ($f = 0.91$; $p > 0.05$) (Appendix 3a).

The protein content in the hepatopancreas of the juveniles ranged from 55.4% to 58.3% and that of the maturing lobsters from 53.4% to 57.1%. The average protein content in both the size groups ranged from 55.4% (I fortnight of December) to 57.6% (I fortnight of February), the fortnightly variations did not follow any trend (Fig. 10b) and the variations were not significantly different ($f = 0.80$; $p > 0.05$) (Appendix 3b).

The protein content in the exoskeleton of the juveniles ranged from 2.8% to 3.9% and that of the maturing lobsters from 2.6% to 3.9%. The average protein content in both the size groups ranged from 3.0% (I fortnights of June and July) to 3.9% (I fortnight of May and II fortnights of March and July). Eventhough a definite fortnightly trend was

Fig. 10. Fortnightly variation in the protein content of tail muscle, hepatopancreas and exoskeleton of *P. homarus* from February 1999 to January 2000

Fig. 10a

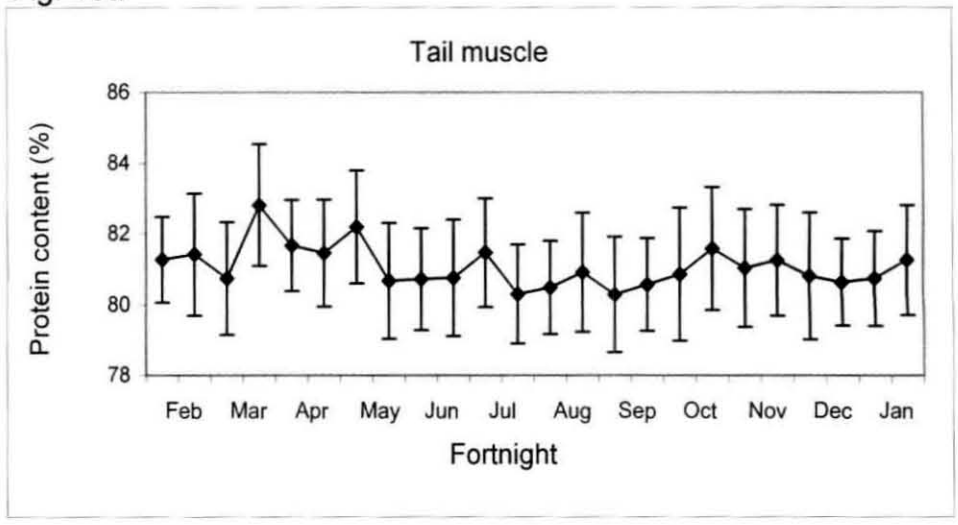


Fig. 10b

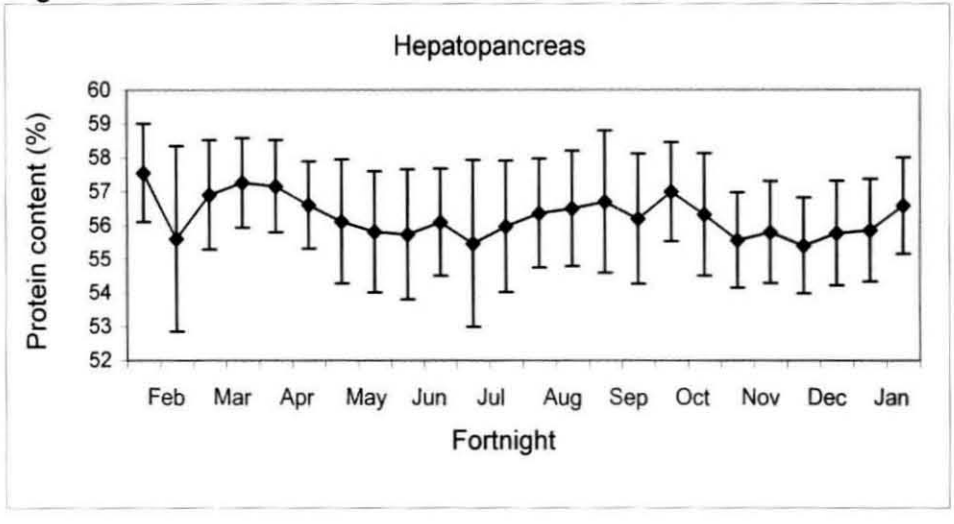
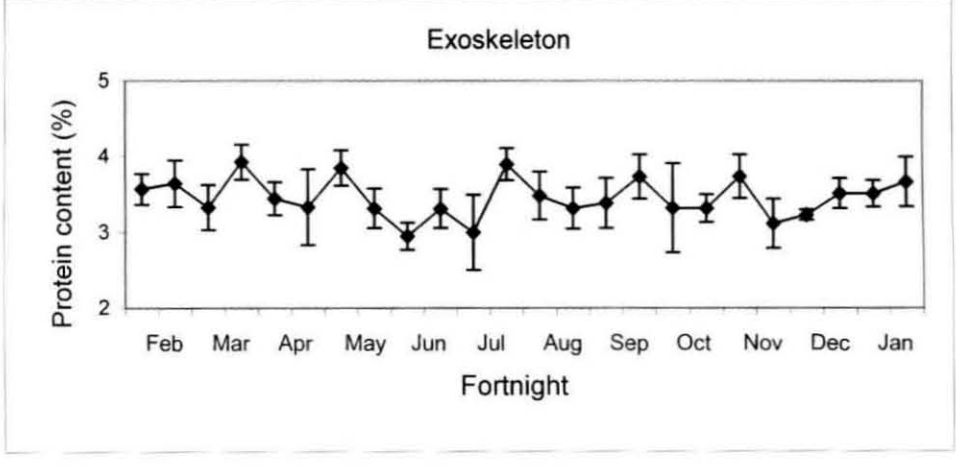


Fig. 10c



not evident (Fig. 10c), the variations were significantly different ($f = 4.49$; $p < 0.01$) (Appendix 3c).

4.1.5.3 Lipid

The lipid content in the tail muscle of the juveniles ranged from 8.5% to 12.2% and that of the maturing lobsters from 8.4% to 12.2% in the fortnightly samples collected during February 1999 to January 2000. The average lipid content in both the size groups ranged from 8.8% (I fortnight of September) to 12.2% (I fortnight of July). Eventhough a definite fortnightly trend was not evident (Fig. 11a), the variations were significantly different ($f = 5.39$; $p < 0.01$) (Appendix 4a).

The lipid content in the hepatopancreas of the juvenilies ranged from 27.8% to 32.3% and that of the maturing lobsters from 28.2% to 35.5%. The average lipid content in both the size groups ranged from 28.6% (I and II fortnights of August) to 33.6% (I fortnight of November). Eventhough a definite fortnightly trend was not evident (Fig. 11b), the variations were significantly different ($f = 1.63$; $p < 0.05$) (Appendix 4b).

The lipid content in the exoskeleton of the juveniles ranged from 0.9% to 1.3% and that of the maturing lobsters from 0.7% to 1.1%. The average lipid content in both the size groups ranged from 0.8% (I fortnight of November and II fortnight of April) to 1.2% (I fortnight of January and II fortnight of November). Eventhough a definite fortnightly trend was not evident (Fig. 11c), the variations were significantly different ($f = 2.15$; $p < 0.01$) (Appendix 4c).

4.1.5.4 Carbohydrate

The fortnightly carbohydrate content in the tail muscle of both the juvenile and maturing lobsters ranged from 1.0% to 2.1%. The average carbohydrate content in both the size groups ranged from 1.1% (II fortnight of March) to 2.0% (I fortnight of June and II fortnights of May and December). Eventhough a definite fortnightly trend was not evident

Fig. 11. Fortnightly variation in the lipid content of tail muscle, hepatopancreas and exoskeleton of *P. homarus* from February 1999 to January 2000

Fig. 11a

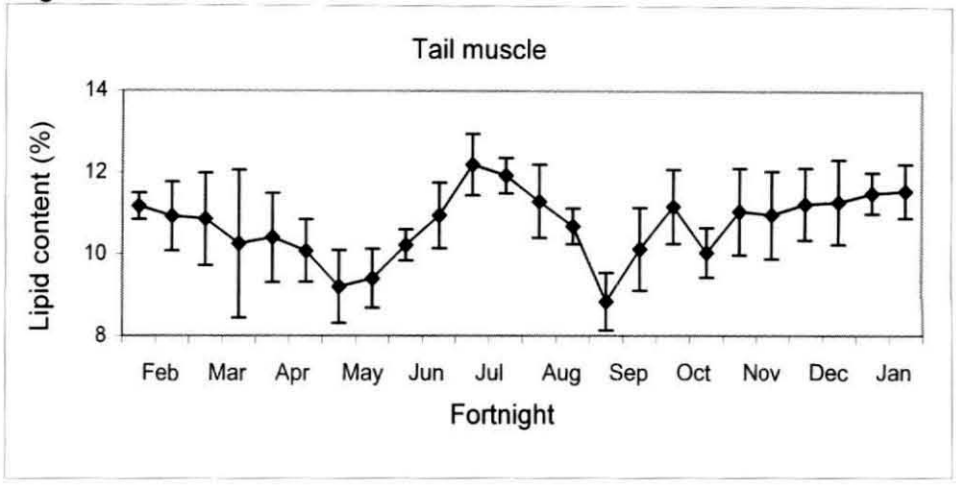


Fig. 11b

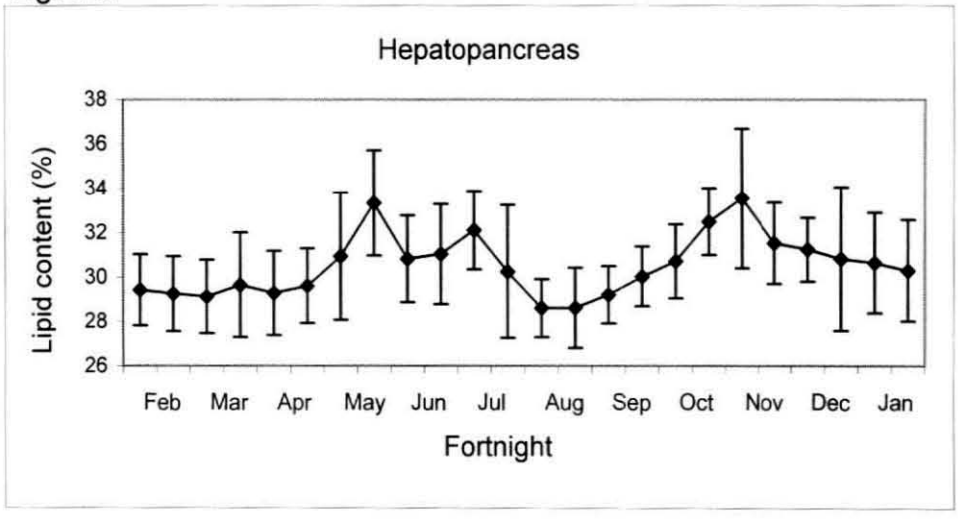
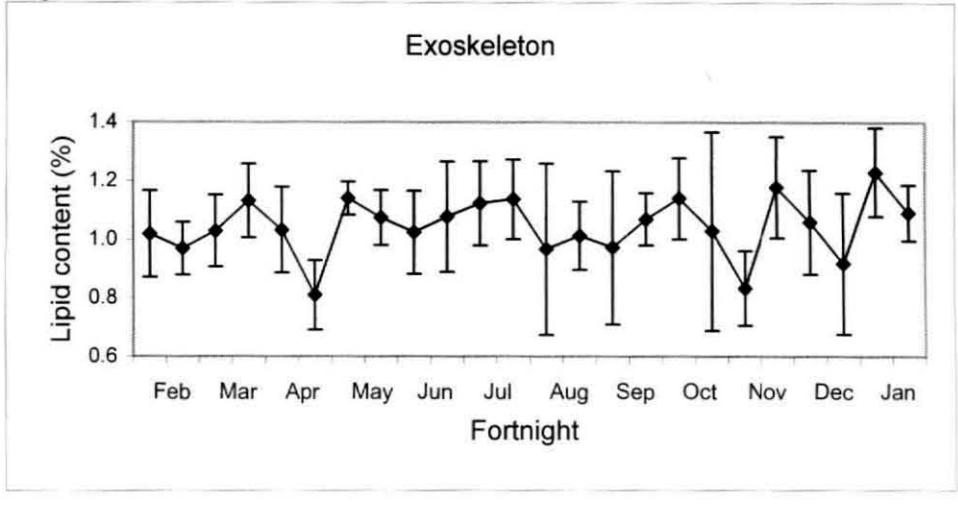


Fig. 11c



(Fig. 12a), the variations were significantly different ($f = 7.04$; $p < 0.01$) (Appendix 5a).

The fortnightly carbohydrate content in the hepatopancreas of the juveniles ranged from 4.1% to 6.9% and that of the maturing lobsters from 4.9% to 6.9%. The average carbohydrate content in both the size groups ranged from 4.7% (II fortnight of March) to 6.7% (II fortnight of November). Eventhough a definite fortnightly trend was not evident (Fig. 12b), the variations were significantly different ($f = 7.82$; $p < 0.01$) (Appendix 5b).

The fortnightly carbohydrate content in the exoskeleton of the juveniles ranged from 1.4% to 1.7% and that of the maturing lobsters from 1.6% to 2.0%. The average carbohydrate content in both the size groups ranged from 1.5% (II fortnights of August and November) to 1.9% (I fortnights of January and May and II fortnight of May). Eventhough a definite fortnightly trend was not evident (Fig. 12c), the variations were significantly different ($f = 1.84$; $p < 0.01$) (Appendix 5c).

4.1.5.5 Ash

The ash content in the tail muscle of the juveniles ranged from 7.4% to 11.4% and that of the maturing lobsters from 7.0% to 10.1%. The average ash content in both the size groups ranged from 7.2% (I fortnight of July) to 10.3% (I fortnight of September). The fortnightly fluctuations did not follow any specific trend (Fig. 13a). However, the differences between the fortnightly samples were significantly different ($f = 2.77$; $p < 0.01$) (Appendix 6a).

The fortnightly ash content in the hepatopancreas of the juveniles ranged from 4.8% to 7.2% and that of the maturing lobsters from 5.2% to 7.8%. The average ash content in both the size groups ranged from 5.3% (I fortnight of July and II fortnights of June and December) to 7.2% (II fortnight of January). Eventhough a definite fortnightly trend was not evident (Fig. 13b), the variations were significantly different ($f = 3.31$; $p < 0.01$) (Appendix 6b).

Fig. 12. Fortnightly variation in the carbohydrate content of tail muscle, hepatopancreas and exoskeleton of *P. homarus* from February 1999 to January 2000

Fig. 12a

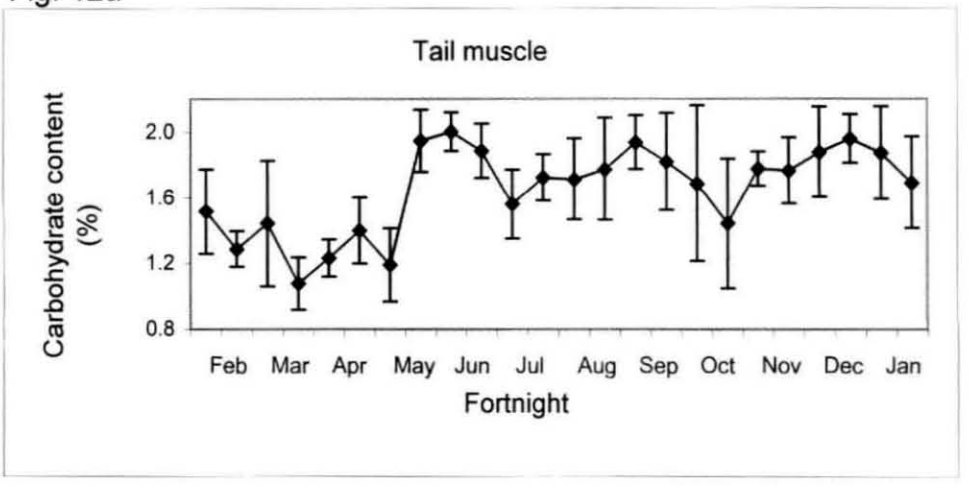


Fig. 12b

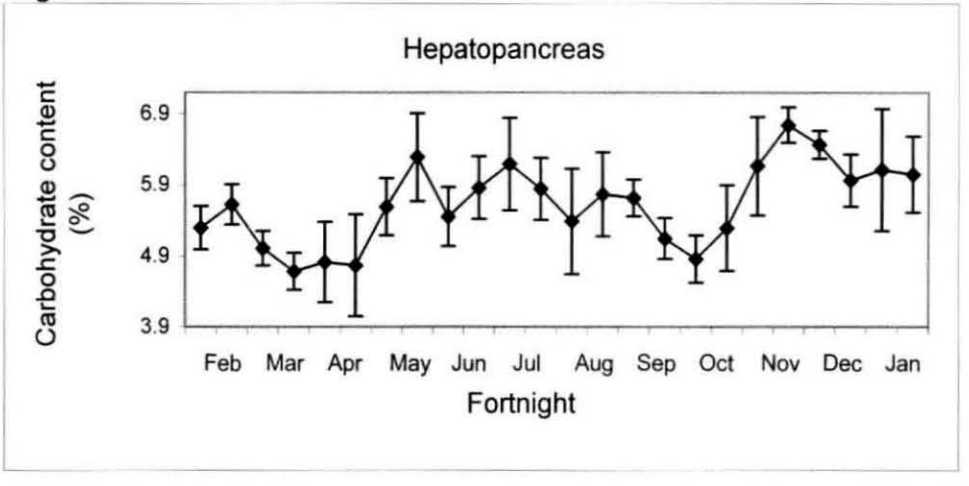


Fig. 12c

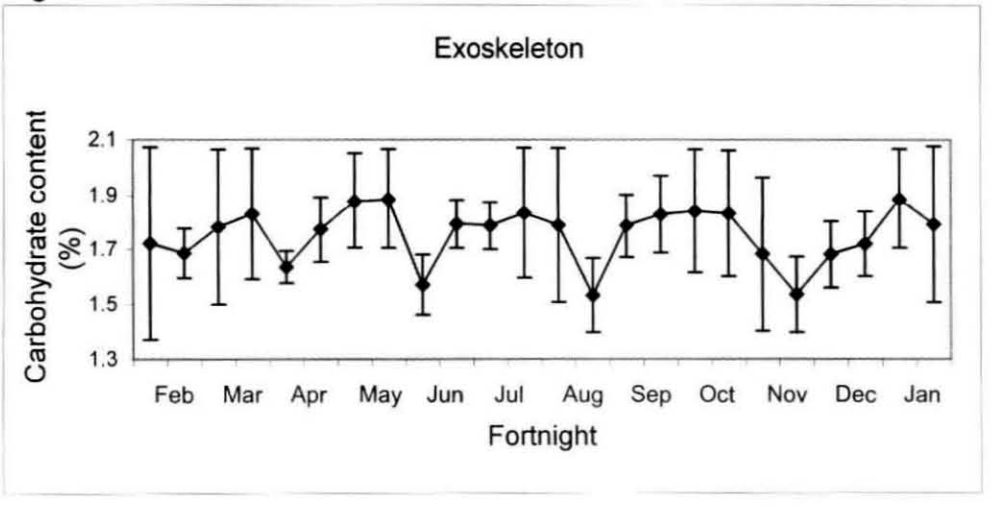


Fig. 13. Fortnightly variation in the ash content of tail muscle, hepatopancreas and exoskeleton of *P. homarus* from February 1999 to January 2000

Fig. 13a

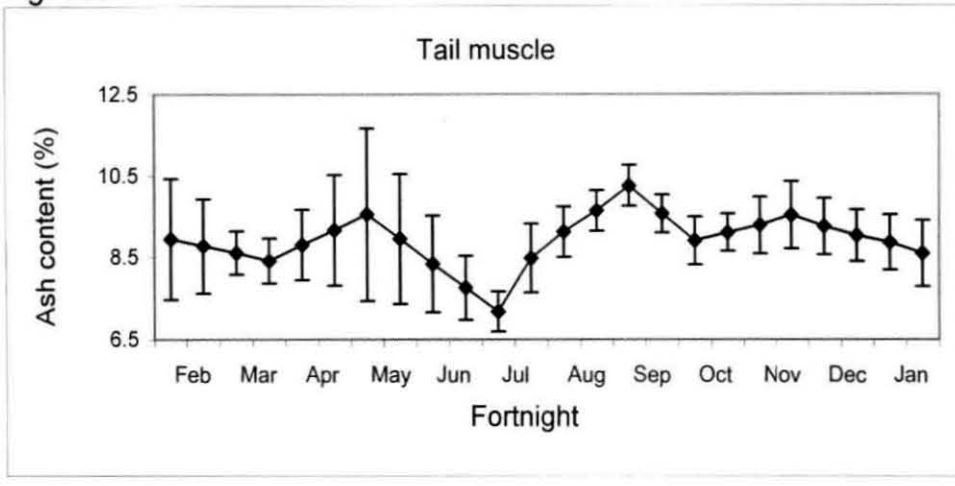


Fig. 13b

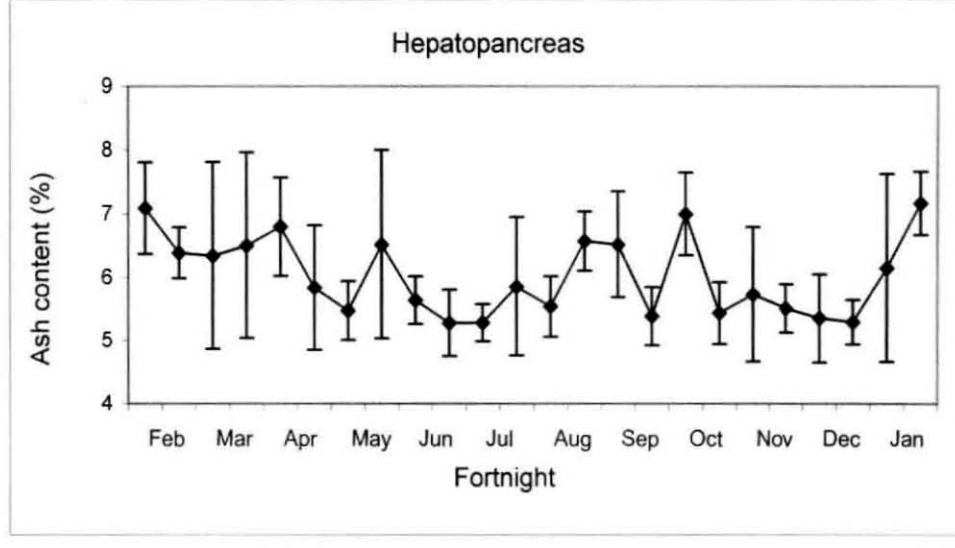
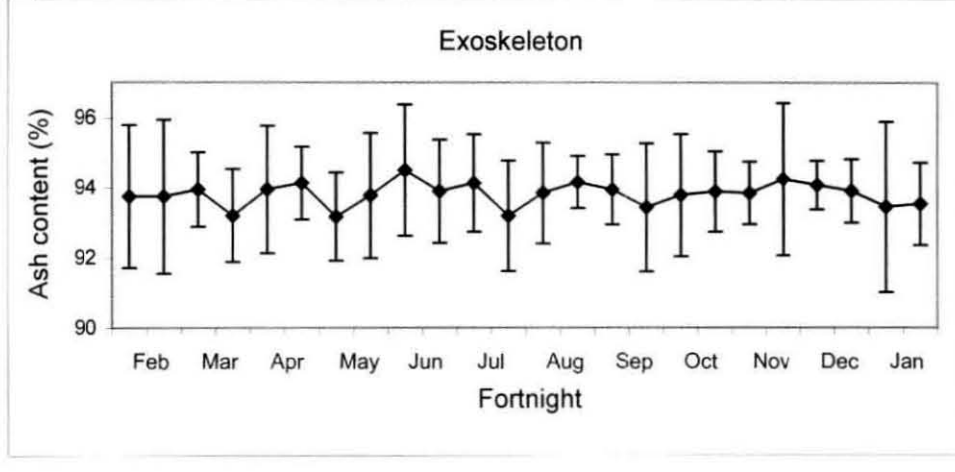


Fig. 13c



The ash content in the exoskeleton of the juveniles ranged from 93.9% to 94.5% and that of the maturing lobsters from 93.0% to 94.6% in the fortnightly samples collected during February 1999 to January 2000. The average ash content in both the size groups ranged from 93.2%(I fortnight of May and II fortnights of March and July) to 94.5% (I fortnight of June). The fortnightly fluctuations did not follow any specific trend (Fig. 13c); the ANOVA indicated that the differences between the fortnightly samples were not significantly different (f 0.29; $p > 0.05$) (Appendix 6c).

4.1.5.6 Energy

The energy content in the tail muscle of the juveniles ranged from 19.9 kj/g to 21.9 kj/g and that of the maturing lobsters from 19.7 kj/g to 22.2 kj/g. The average energy content in both the size groups ranged from 19.9 kj/g (I fortnight of September) to 22.0 kj/g (I fortnight of July). Eventhough a definite fortnightly trend was not evident (Fig. 14a), the variations were significantly different ($f = 3.89$; $p < 0.01$) (Appendix 7a).

The energy content in the hepatopancreas of the juveniles ranged from 23.7 kj/g to 25.8 kj/g and that of the maturing lobsters from 23.2 kj/g to 26.3 kj/g. The average energy content in both the size groups ranged from 23.8 kj/g (II fortnights of February and August) to 25.7 kj/g (I fortnight of November). The fortnightly fluctuations did not follow any specific trend (Fig. 14b). However, the differences between the fortnightly samples were significantly different ($f = 2.97$; $p < 0.01$) (Appendix 7b).

The energy content in the exoskeleton of both the juveniles and maturing lobsters ranged from 0.06 kj/g to 0.11 kj/g in the fortnightly samples collected during February 1999 to January 2000. The average energy content in both the size groups ranged from 0.07 kj/g (I fortnight of June) to 0.11 kj/g (I fortnight of May and II fortnights of March and July). The fortnightly variations did not follow any specific trend (fig. 14c) and the variations were not significantly different ($f = 0.99$; $p > 0.05$) (Appendix 7c).

Fig. 14. Fortnightly variation in the energy content of tail muscle, hepatopancreas and exoskeleton of *P. homarus* from February 1999 to January 2000

Fig. 14a

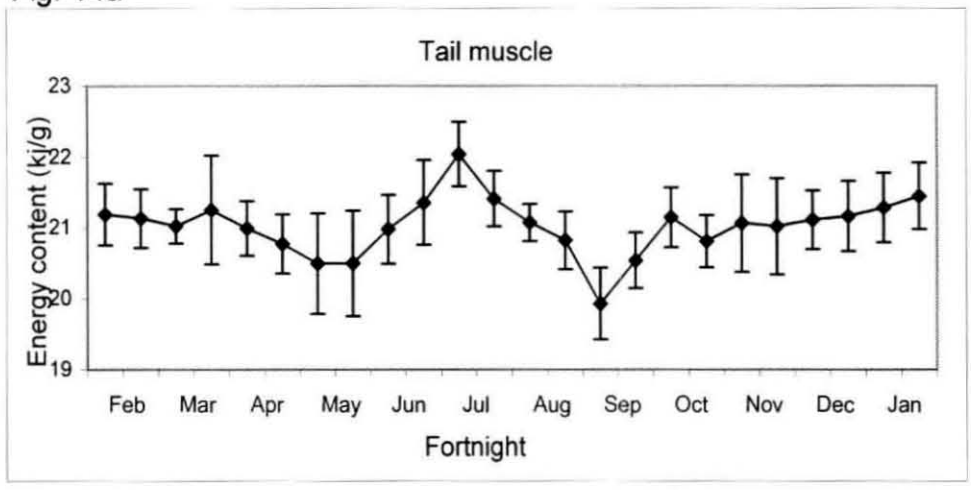


Fig. 14b

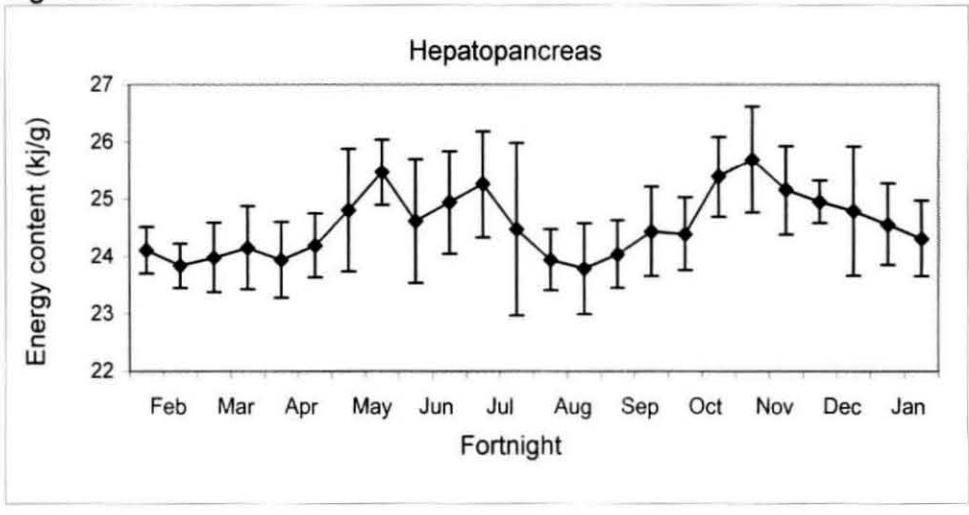
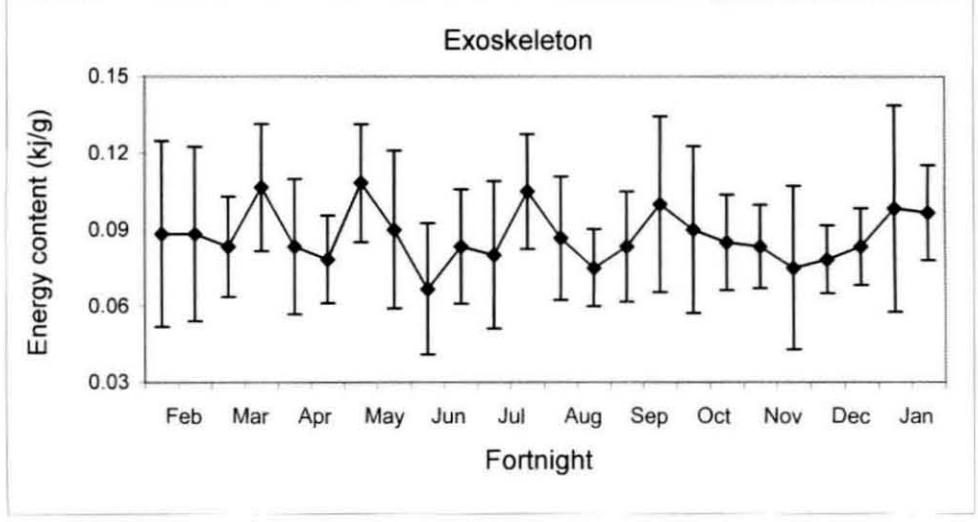


Fig. 14c



4.1.6 Comparison of proximate composition and energy content between tissues

For the comparison of the proximate composition and energy content of the muscle, hepatopancreas and exoskeleton of *P. homarus*, the annual average values of the juveniles and adults were pooled and analysed.

4.1.6.1 Water content

The mean water content greatly differed between the muscle (75.9%), hepatopancreas (63.7%) and exoskeleton (37.7%) of the lobster (Table 13). The values between the muscle and hepatopancreas ($t = 31.52$; $p < 0.01$); between the hepatopancreas and exoskeleton ($t = 71.99$; $p < 0.01$); and between the muscle and exoskeleton ($t = 99.77$; $p < 0.01$) were significantly different (Table 14).

4.1.6.2 Protein

The mean protein content greatly differed between the muscle (81.1%), hepatopancreas (56.3%) and exoskeleton (3.5%) of the lobster (Table 13). The difference in the values between the muscle and hepatopancreas ($t = 114.64$; $p < 0.01$); between the hepatopancreas and exoskeleton ($t = 292.64$; $p < 0.01$); and between the muscle and exoskeleton ($t = 622.66$; $p < 0.01$) were significantly different (Table 14).

4.1.6.3 Lipid

The mean lipid content greatly differed between the muscle (9.8%); hepatopancreas (31.6%); and exoskeleton (1.0%) of the lobster (Table 13). The values between the muscle and hepatopancreas ($t = 72.63$; $p < 0.01$); between the hepatopancreas and exoskeleton ($t = 115.83$; $p < 0.01$); and between the muscle and exoskeleton ($t = 59.16$; $p < 0.01$) were significantly different (Table 14).

Table 13. Average proximate composition (% dry weight) and energy content (kj/g) in the tail muscle, hepatopancreas and exoskeleton of *P. homarus* during February 1999 to January 2000 (pooled values of juvenile and mature lobsters); ± indicates standard deviation

TISSUE	WATER	PROTEIN	LIPID	CARBO-HYDRATE	ASH	ENERGY
TAIL MUSCLE	75.9 ± 2.0	81.1 ± 0.8	9.8 ± 1.0	1.7 ± 0.3	7.4 ± 1.0	21.0± 0.5
HEPATOPANCREAS	63.7 ± 1.8	56.3 ± 1.2	31.6 ± 1.8	5.6 ± 0.7	6.5 ± 0.9	24.6 ± 0.7
EXOSKELETON	37.7 ± 1.7	3.5 ± 0.3	1.0 ± 0.2	1.7 ± 0.2	93.8 ± 0.4	0.09 ± 0.01

Table 14. Results of the Students t test between different tissues of *P. homarus*

TISSUE	Student`s t test	WATER	PROTEIN	LIPID	CARBOHY-DRATE	ASH	ENERGY
MUSCLE & HEPATOPANCREAS	p value	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
	t value	31.52	114.64	72.63	36.21	4.53	28.69
HEPATOPANCREAS & EXOSKELETON	p value	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
	t value	71.99	292.64	115.83	36.73	607.68	240.02
MUSCLE & EXOSKELETON	p value	<0.01	<0.01	<0.01	>0.05	<0.01	<0.01
	t value	99.77	622.66	59.16	0.00	549.96	286.65

4.1.6.4 Carbohydrate

The mean carbohydrate content greatly differed between the muscle (1.7%), hepatopancreas (5.6%) and exoskeleton (1.7%) of the lobster (Table 13). The values between the muscle and hepatopancreas ($t = 36.21$; $p < 0.01$); and between the hepatopancreas and exoskeleton ($t = 36.73$; $p < 0.01$) were significantly different (Table 14).

4.1.6.5 Ash

The mean ash content greatly differed between the muscle (7.4%), hepatopancreas (6.5%) and exoskeleton (93.8%) of the lobster (Table 13). The values between the muscle and hepatopancreas ($t = 4.53$; $p < 0.01$); between the hepatopancreas and exoskeleton ($t = 607.68$; $p < 0.01$); and between the muscle and exoskeleton ($t = 549.96$; $p < 0.01$) were significantly different (Table 14).

4.1.6.6 Energy content

The mean energy content greatly differed between the muscle (21.0 kj/g), hepatopancreas (24.6 kj/g) and exoskeleton (0.09 kj/g) of the lobster (Table 13). The values between the muscle and hepatopancreas ($t = 28.69$; $p < 0.01$); between the hepatopancreas and exoskeleton ($t = 240.02$; $p < 0.01$); and between the muscle and exoskeleton ($t = 286.65$; $p < 0.01$) were significantly different (Table 14).

4.2 Effect of starvation

4.2.1 Survival

The starved, control lobsters survived for an average of 97.0 $\pm$ 5.3 days, whereas the starved, bilaterally eyestalk ablated lobsters survived for only 48.3 $\pm$ 4.8 days. The difference in the average survival period between the control and ablated lobsters was highly significant ($t = 13.75$; $p < 0.01$). All the control lobsters survived upto 12 weeks of food deprivation. Among the four lobsters that remained (the rest were sacrificed in the I, II, III, VI, IX weeks of starvation) after 9 weeks of

sampling, one lobster died in the 13th week, one in the 14th week and two in the 15th week. Among the starved, ablated lobsters, 6 lobsters died in the 7th week itself and the remaining 2 lobsters in the 8th week.

4.2.2 Moulting

None of the control lobsters moulted during the starvation period of 15 weeks. On the other hand, 3 ablated lobsters moulted once in the 7th and 8th week of starvation. One of the moulted lobsters died in the 7th week (46th day) and two more on the 8th week (51st & 52nd day) of food deprivation.

4.2.3 Hepatosomatic Index (HSI_d)

The dry hepatosomatic index (HSI_d) decreased from 4.72 % (at the commencement of starvation) to 1.75 % (15 weeks of starvation) in the control lobsters (Fig. 15). In the ablated lobsters, the hepatosomatic index steeply declined to 1.64 % in the 8th week itself. Decline in the hepatosomatic index was maximum between 3 and 6 weeks of starvation in both the groups. When the lobsters succumbed to death due to starvation, the HSI_d was almost equal for the control (1.75 %) as well as for the ablated (1.64 %) groups. The decline in HSI_d was strongly related to the duration of starvation. The following regression equations can be used for estimating the HSI_d of the control and ablated *P. homarus* during different weeks of starvation:

control: $y = 4.40 - 0.20 x$; $r = 0.9490$

ablated: $y = 4.66 - 0.42 x$; $r = 0.9878$

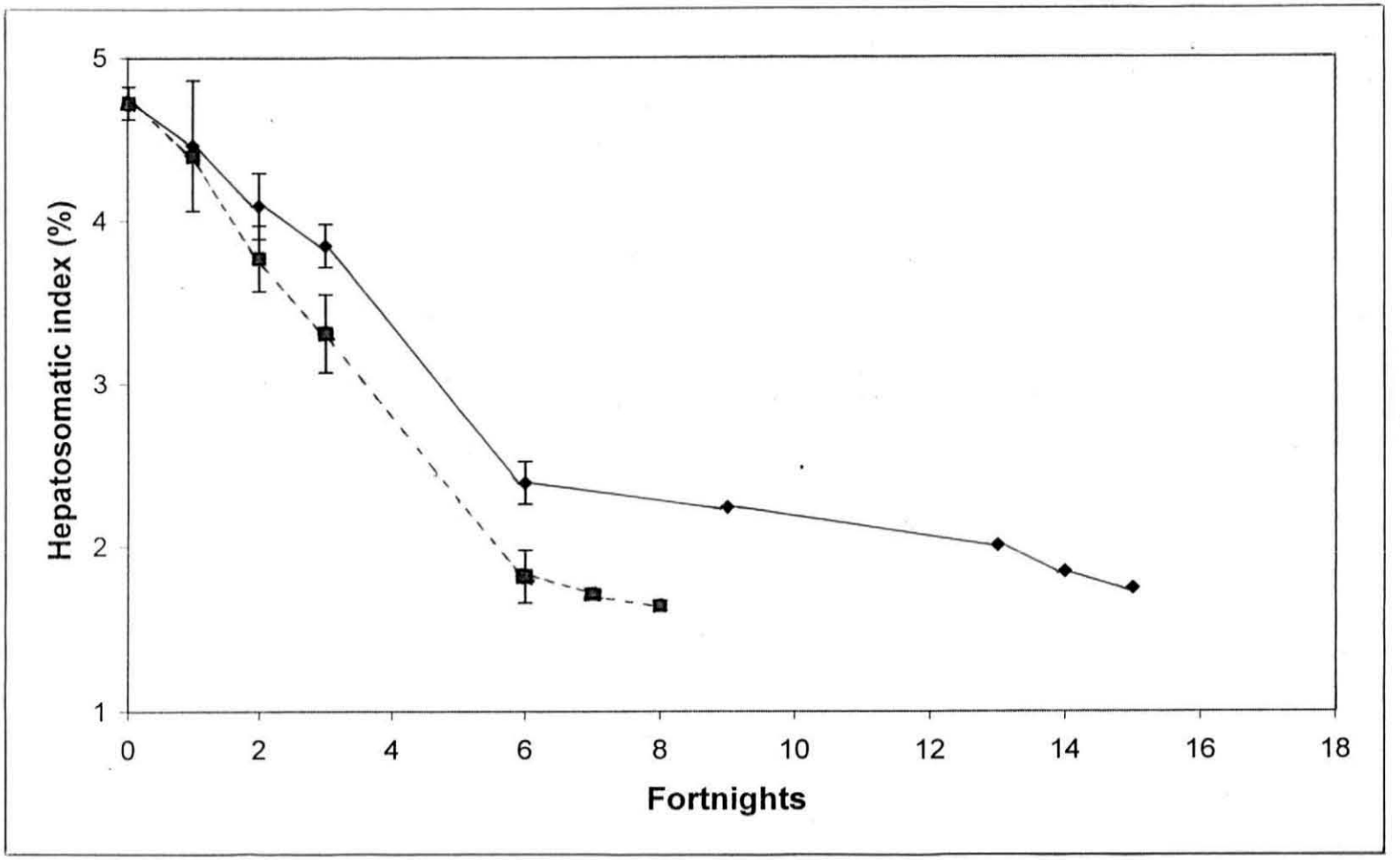
where, $y = HSI_d$

x = weeks of starvation

4.2.4 Weight loss

The mean wet body weight of the control lobsters decreased from 110.8 g at the commencement of the experiment to 69.7 g at the

Fig. 15. Effect of starvation on the Hepatosomatic index of *P. homarus*



time of death (15 weeks). The weight loss during 15 weeks of starvation was 41.1 g (Table 15). The lobster lost 37.1 % of its initial wet weight due to starvation at the time of death. The control lobsters lost 0.42 g/day during 6th week of starvation (Fig. 16) or 0.50% body weight/day during 6th week of starvation (Fig. 17) and the rate of body weight loss did not increase thereafter until death.

The mean wet weight of the starved ablated lobster decreased from 134.0 g at the commencement of the experiment to 94.3 g at the time of death (8 weeks). The weight loss during the 8 weeks of starvation was 39.7g (Table 16). The ablated lobster moulted (average wet weight of the moult = 29.5 g) during this period and the loss of weight including moult was 69.2 g. The wet weight lost during the 8 weeks of starvation by the ablated lobster was almost equal to that by the control lobster during 14 weeks of starvation. The ablated lobsters lost 29.6 % of wet weight excluding the moult. Considering the moult as a part of the growth process, the actual weight loss in the ablated lobster was only 7.61% (10.2 g) of the initial wet weight. The rate of weight loss in the ablated lobsters at the time of death was 0.73 g/day excluding the moult and 1.3 g/day including the moult (Fig. 16). The corresponding loss was 0.54 %/day excluding the moult and 0.94 %/day including the moult (Fig. 17).

4.2.5 Proximate composition and energy contents

4.2.5.1 Tail muscle

The water content in the muscle of the control lobster increased from 72.9 % in the first day of starvation to 79.4 % in the 15th week of starvation (Fig. 18). In the ablated lobsters, the increase was steeper and the water content reached 85.5 % in the 8th week of starvation (Fig. 18). The increase in water content in the control ($f = 43.89$; $p < 0.01$) (Appendix 8a) and ablated lobsters ($f = 71.49$; $p < 0.01$) (Appendix 8b) was highly significant. The water content increased gradually upto 6th week but thereafter, the increase was steep in both the

Table 15. Wet weight loss in the control starved *P. homarus*; ± indicates standard deviation

Weeks of starvation	n	Weight loss	
		g	% of initial body weight
0	4	0.0 ± 0.00	0.00 ± 0.00
1	4	0.00 ± 0.00	0.00 ± 0.00
2	4	0.62 ± 0.06	0.71 ± 0.11
3	4	2.66 ± 0.15	2.85 ± 0.17
6	4	17.54 ± 1.03	21.14 ± 0.37
9	4	26.39 ± 2.28	21.05 ± 1.19
13	1	35.13	33.42
14	1	38.43	36.37
15	2	41.14	37.12

Fig. 16 Effect of starvation on weight loss (g/day) in *P. homarus*

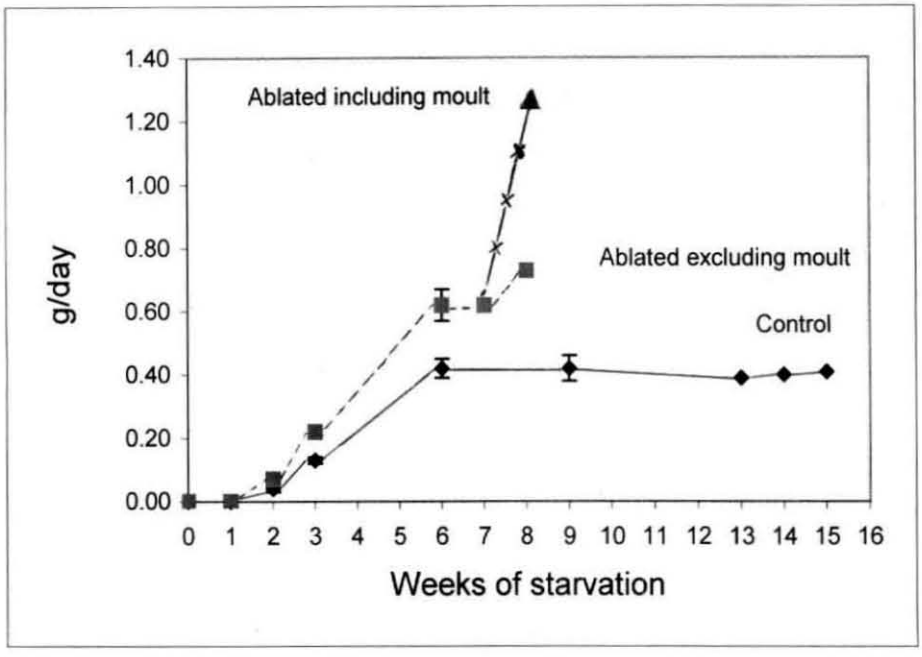


Fig. 17 Effect of starvation on weight loss (%/day) in *P. homarus*

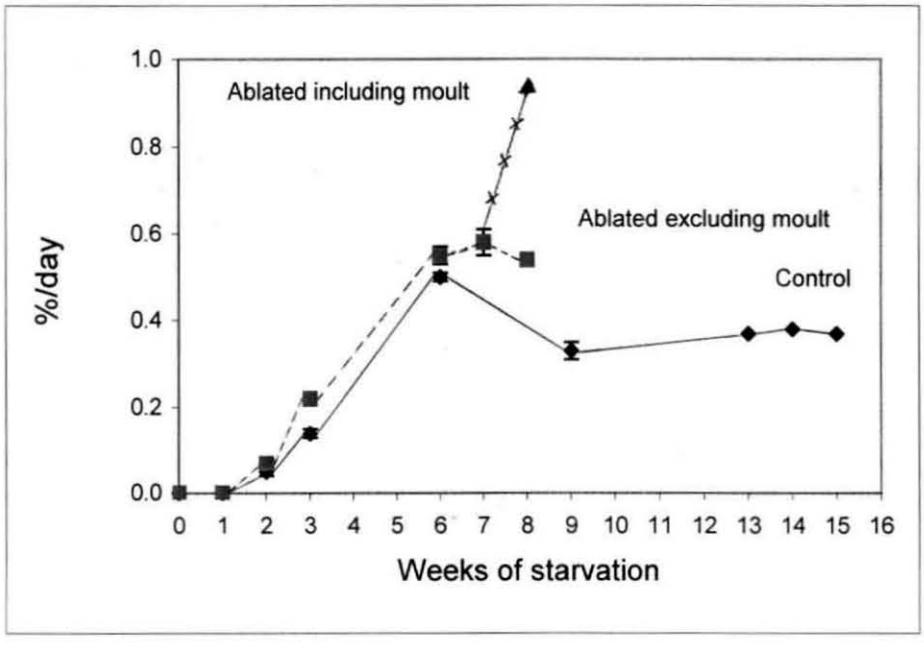


Table 16. Wet weight loss in the ablated starved *P. homarus*; ± indicates standard deviation

Weeks of starvation	n	Weight loss			
		Excluding moult		Including moult	
		g	% of initial body weight	g	% of initial body weight
0	4	0.0 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
1	4	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
2	4	0.95 ± 0.08	0.92 ± 0.06	0.95 ± 0.08	0.92 ± 0.06
3	4	4.59 ± 0.16	4.58 ± 0.08	4.59 ± 0.16	4.58 ± 0.08
6	4	26.17 ± 1.89	23.37 ± 0.85	26.17 ± 1.89	23.37 ± 0.85
7	6	28.46 ± 2.1	26.63 ± 0.74	28.46 ± 2.1*	26.63 ± 0.74*
8	2	39.66	29.61	69.16	51.63

* Since only one lobster moulted during the 7th week, the weight loss the including moult was not calculated

Fig. 18. Effect of starvation on the water content in the tail muscle of *P. homarus*; the vertical lines indicate standard deviation

groups of lobsters. ANOCOVA showed a significant difference ($f = 126.01$; $p < 0.01$) in the mean water content of the tail muscle between the control and ablated lobsters (Table 17).

Surprisingly, the protein content in the control lobster increased from 80.5 % to 84.1 % in terms of dry weight of the muscle (Fig. 19), which is a highly significant increase ($f = 7.17$; $p < 0.01$) (Appendix 9a). However, the protein content of the ablated lobster decreased from 80.5 % to 78.4 % in 8 weeks (Fig. 19) ($f = 3.74$; $p < 0.05$) (Appendix 9b). The ANOCOVA showed significant difference in the tail muscle protein ($f = 16.40$; $p < 0.01$) (Table 17) between the control and ablated lobsters.

The lipid content decreased by 40 to 50 % in the control and ablated lobsters in terms of dry weight. At the time of death, the lipid content was 5.1 % and 6.1 % in the control and ablated lobsters, respectively (Fig. 20). The weekly decrease in the lipid content of the control ($f = 117.64$; $p < 0.01$; Appendix 10a) and ablated ($f = 68.14$; $p < 0.01$; Appendix 10b) lobsters was highly significant. The ANOCOVA showed a significant difference in the mean lipid content between control and ablated lobsters in terms of dry weight ($f = 23.06$; $p < 0.01$) (Table 17) at the time of death.

The carbohydrate content decreased from 1.9 % to 1.1 % in the control lobster, and to 1.7 % in the ablated lobsters (Fig. 21). The weekly decrease was significantly different in the control ($f = 53.61$; $p < 0.01$; Appendix 11a) and ablated ($f = 4.43$; $p < 0.01$; Appendix 11b) lobsters. The ANOCOVA showed significant difference in the carbohydrate content between the control and ablated lobsters ($f = 11.41$; $p < 0.01$) (Table 17) at the time of death.

Steady increase in the ash content was observed in the control and ablated lobsters. The ash content increased from 7.4 % on the first day of starvation to 9.7 % on the 15^{th} week in the control (Fig. 22) and to 13.8 % in the 8^{th} week in the ablated lobsters. The increase

Table 17. Summary of ANOCOVA between control and ablated *P. homarus* under starvation

Parameter	Tissue	f value	p value
Water content	Tail muscle	126.01	< 0.01
	Hepatopancreas	93.18	< 0.01
	Exoskeleton	1.38	> 0.05
Protein	Tail muscle	16.40	< 0.01
	Hepatopancreas	19.05	< 0.01
	Exoskeleton	31.29	< 0.01
Lipid	Tail muscle	23.06	< 0.01
	Hepatopancreas	50.33	< 0.01
	Exoskeleton	41.72	< 0.01
Carbohydrate	Tail muscle	11.41	< 0.01
	Hepatopancreas	0.45	> 0.05
	Exoskeleton	91.42	< 0.01
Ash	Tail muscle	87.84	< 0.01
	Hepatopancreas	80.29	< 0.01
	Exoskeleton	0.96	> 0.05
Energy	Tail muscle	85.00	< 0.01
	Hepatopancreas	64.52	< 0.01
	Exoskeleton	4.52	< 0.05

Fig. 19. Effect of starvation on the protein content in the tail muscle of *P. homarus*; the vertical lines indicate M66standard deviation

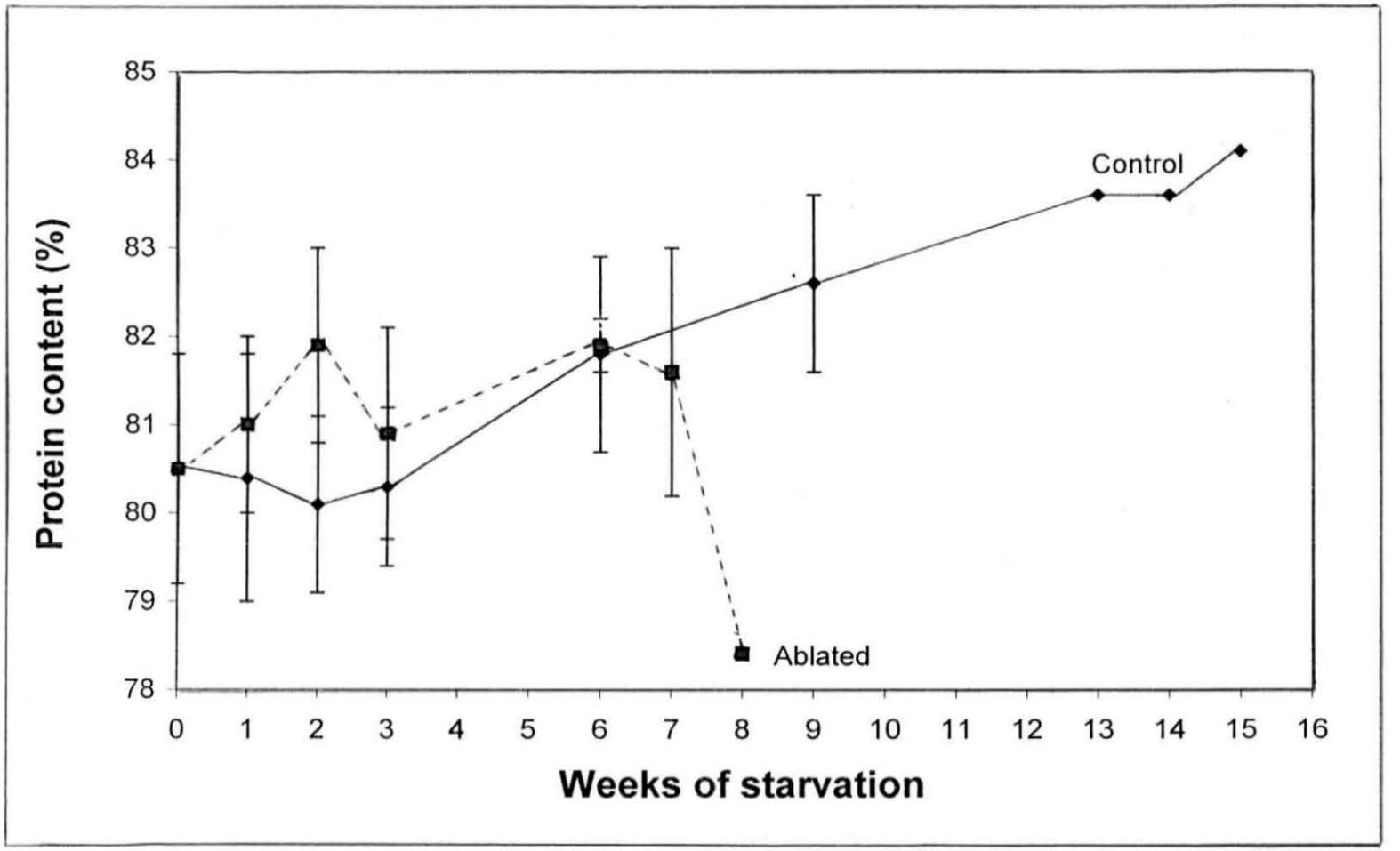


Fig. 20. Effect of starvation on the lipid content in the tail muscle of *P. homarus*; the vertical lines indicate standard deviation

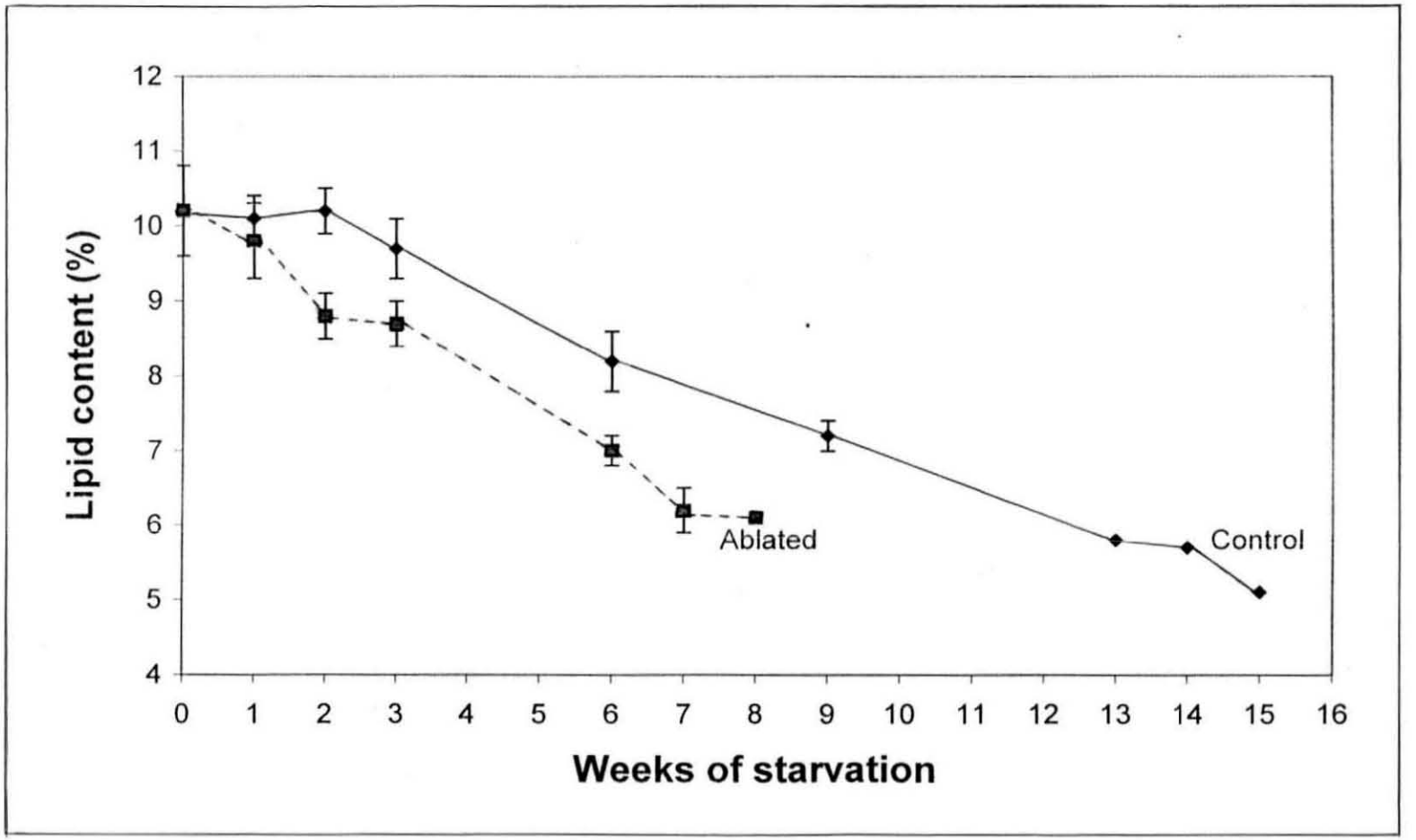


Fig. 21. Effect of starvation on the carbohydrate content in the tail muscle of *P. homarus*; the vertical lines indicate standard deviation

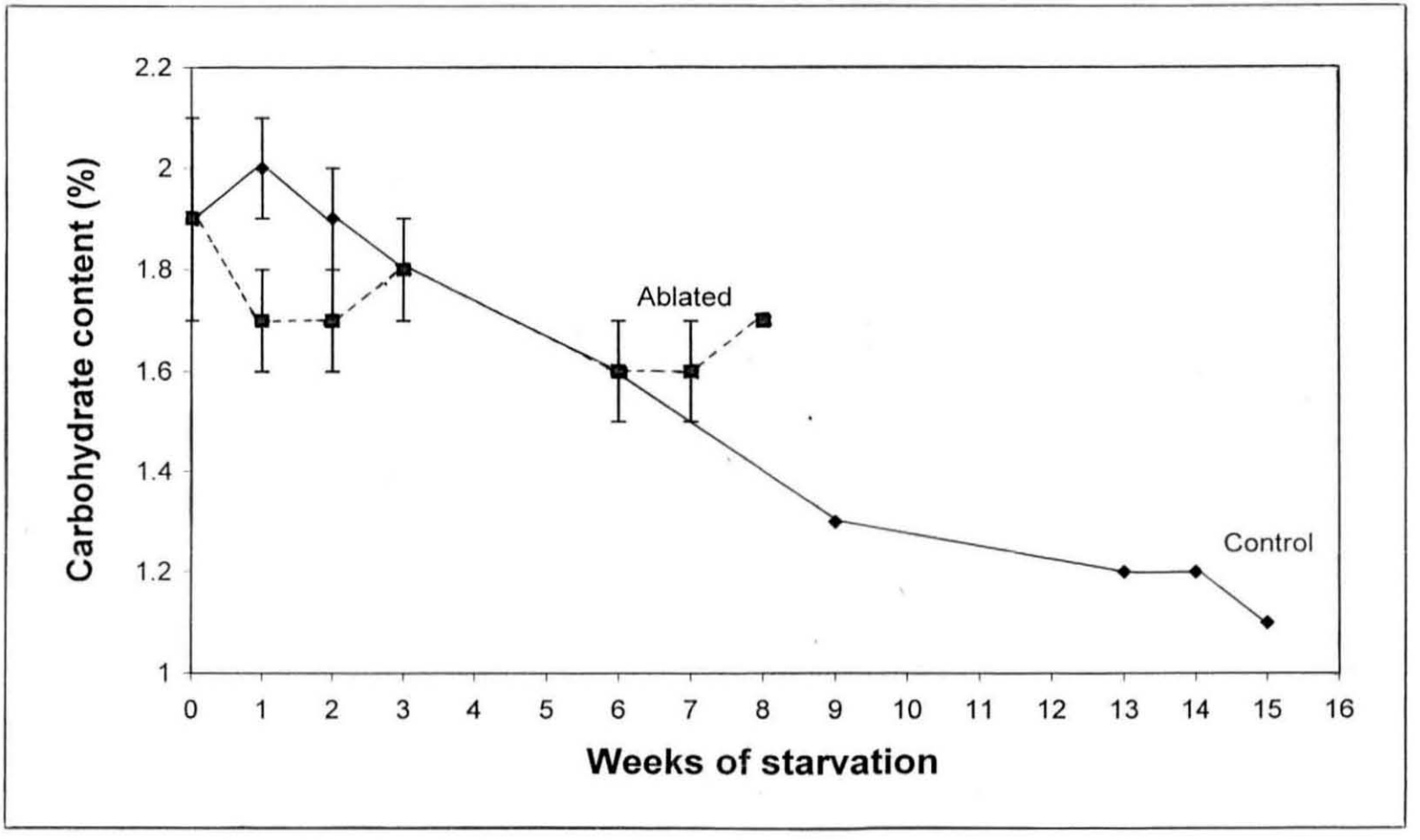
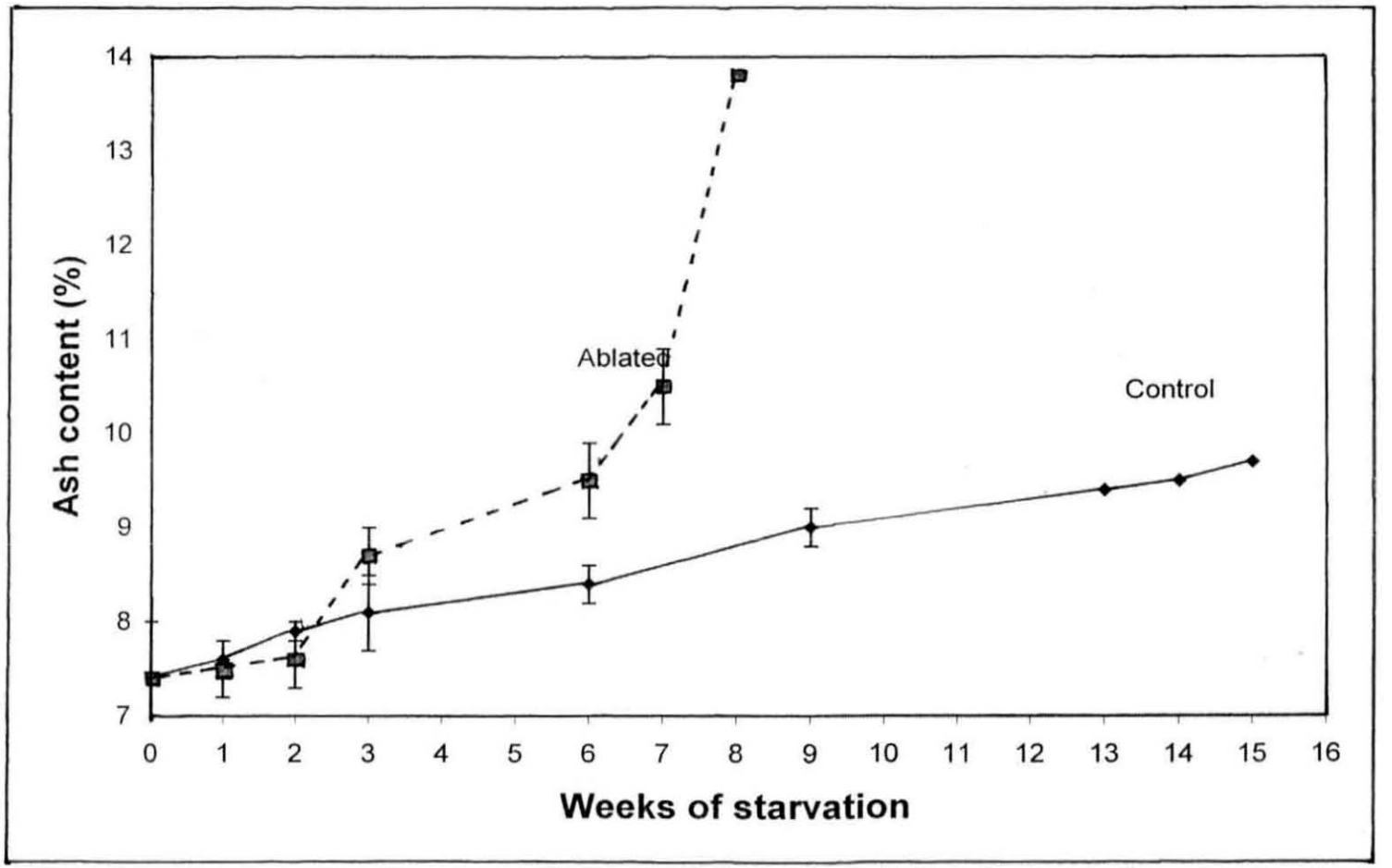


Fig. 22. Effect of starvation on the ash content in the tail muscle of *P. homarus* ; the vertical lines indicate standard deviation



was significant in the control ($f = 15.38$; $p < 0.01$; Appendix 12a) as well as in the ablated ($f = 86.47$; $p < 0.01$; Appendix 12b) lobsters. The ANOCOVA showed significant difference in the ash content ($f = 87.84$; $p < 0.01$) (Table 17) between the control and ablated lobsters at the time of death.

The energy content decreased with the intensification of starvation. It decreased from 21.2 kj/g to 19.4 kj/g in the control (Fig. 23) and to 17.7 kj/g in the ablated lobsters (Fig. 23). The decrease was significantly different ($f = 15.99$; $p < 0.01$) (Appendix 13a) in the control as well as in the ablated ($f = 49.04$; $p < 0.01$) (Appendix 13b) lobsters. The ANOCOVA showed significant difference ($f = 85.00$; $p < 0.01$) (Table 17) in the energy content between the control and ablated groups. The rate of decrease of energy content in the ablated lobster was similar to that of the control lobster upto the 3rd week of starvation, but a sudden decrease was observed thereafter.

4.2.5.2 Hepatopancreas

The water content increased rapidly with the intensity of starvation. It increased from 64.2 % in the first day of starvation to 84.3 % in the control lobster (Fig. 24) and to 87.6 % in the ablated lobster (Fig. 24). Both the groups had almost equal water content (about 78 %) upto 6 weeks of starvation, but a sudden increase was observed in the ablated lobsters from the 6th week. The increase in water content was significantly different in both the control ($f = 81.28$; $p < 0.01$) (Appendix 14a) and ablated ($f = 117.06$; $p < 0.01$) (Appendix 14b) lobsters. The ANOCOVA showed a significant difference ($f = 93.18$; $p < 0.01$) (Table 17) in water content between the control and ablated lobsters.

The increasing trend in the protein content in the tail muscle was observed in the hepatopancreas of the control as well as ablated lobsters. The protein content in the hepatopancreas increased from 55.2 % to 65.2 % in the control (Fig. 25) and ablated lobsters (Fig. 25). The increase was significant in both the control ($f = 40.13$; $p < 0.01$)

Fig. 23. Effect of starvation on the energy content in the tail muscle of *P. homarus* ; the vertical lines indicate standard deviation

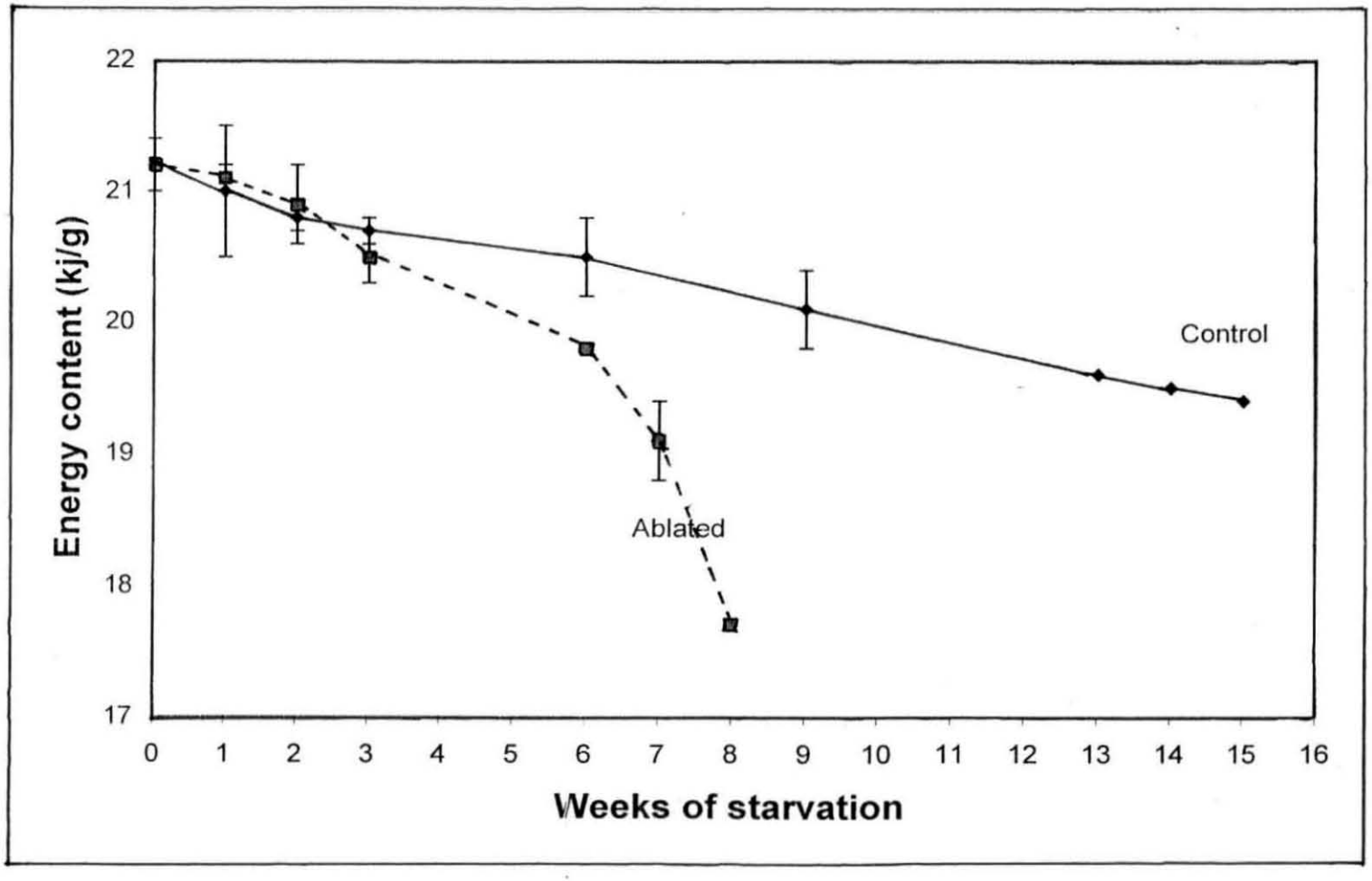


Fig. 24. Effect of starvation on the water content in the hepatopancreas of *P. homarus*; the vertical line indicate standard deviation

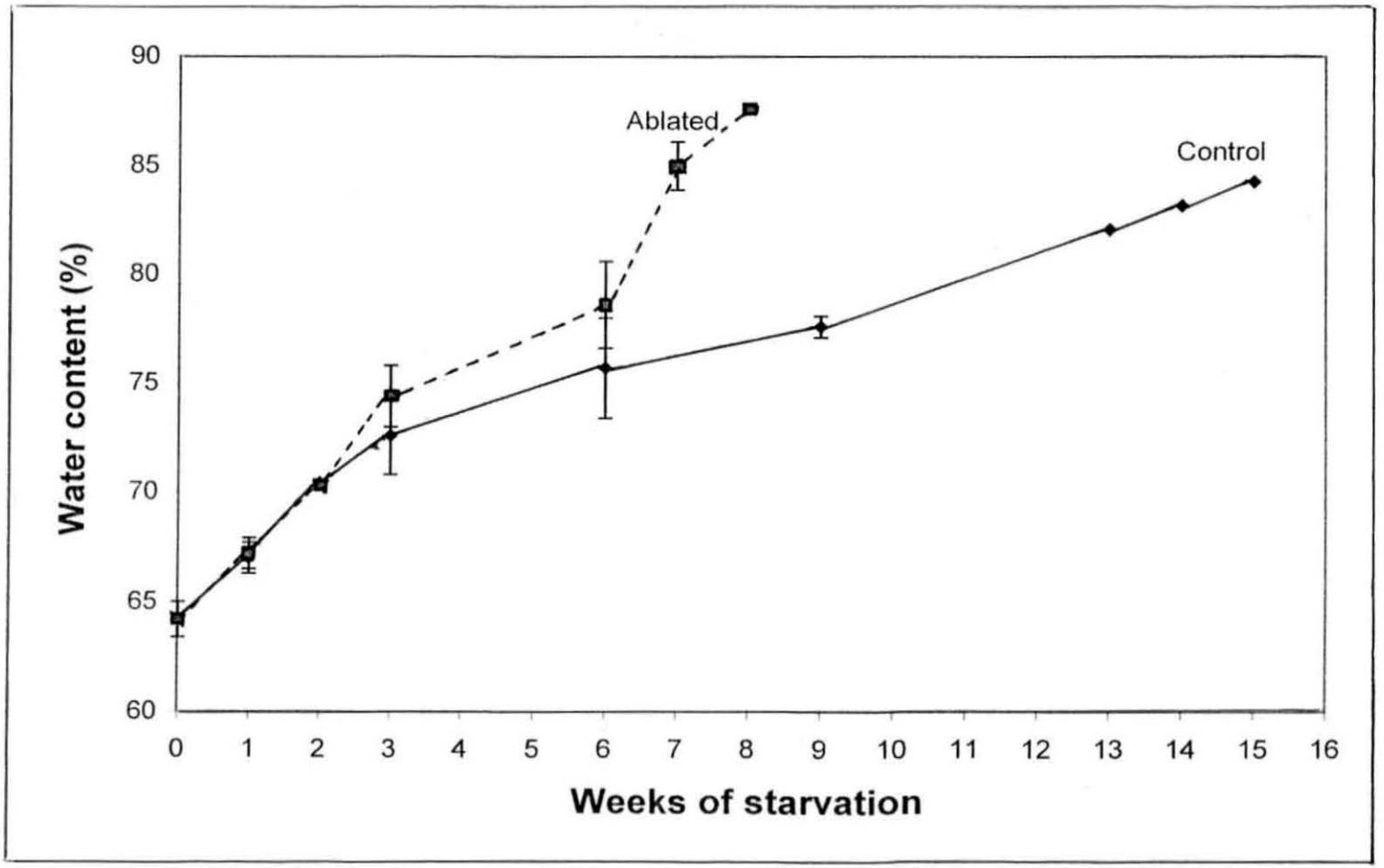
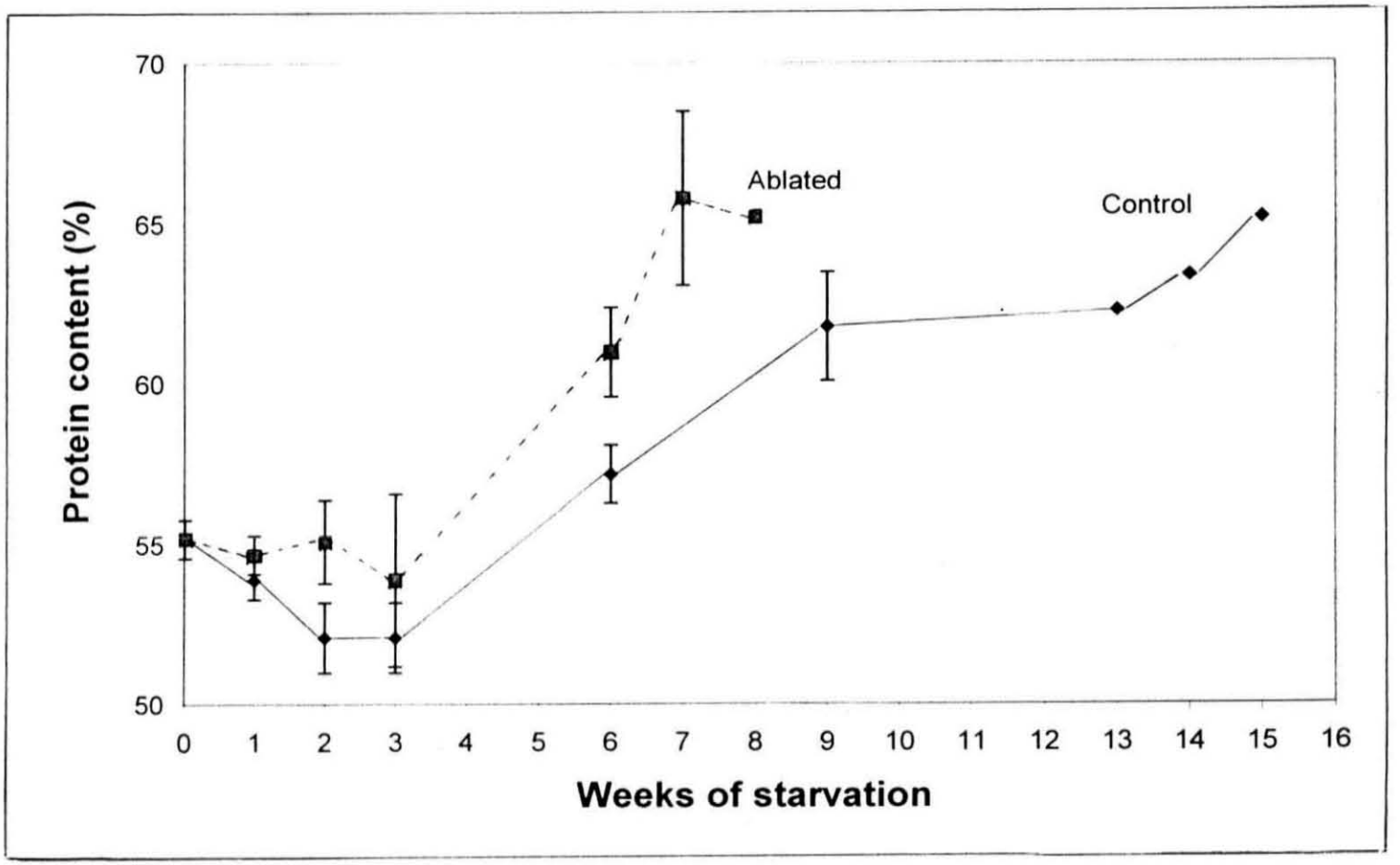


Fig. 25. Effect of starvation on the protein content in the hepatopancreas of *P. homarus*; the vertical lines indicate standard deviation



(Appendix 15a) and ablated ($f = 30.33$; $p < 0.01$) (Appendix 15b) lobsters. The ANOCOVA showed significant difference in the protein content between the control and ablated lobsters ($f = 19.05$; $p < 0.01$) (Table 17).

However, the increase in the protein content was not evident in the quantity of protein in the hepatopancreas. The quantity of protein decreased from 890.4 mg/ 100 g wet body weight at the commencement of the experiment to 217.3 mg/ 100 g on the 15 th week of starvation in the control (Table 18) and to 171.7 mg/ 100 g in the ablated (Table 19) lobsters.

The lipid content decreased sharply with starvation in both the control and ablated lobsters in dry weight basis. It decreased from 33.6 % to 17.6 % in the control (Fig. 26) and to 14.0 % in the ablated groups (Fig. 26). The decrease was significantly different in both the control ($f = 147.22$; $p < 0.01$) (Appendix 16a) and ablated ($f = 228.1$; $p < 0.01$) (Appendix 16b) lobsters. In terms of dry weight, the lipid loss was 47 % in the control and 58 % in the ablated lobsters. The quantity of lipid in the hepatopancreas decreased from 542.4 mg/ 100 g body wet weight to 59.6 mg/ 100 g in the control (Table 18) and to 36.0 mg/ 100 g in the ablated lobsters (Table 19). The ANOCOVA showed a significant difference in the lipid content between the control and ablated lobsters ($f = 50.33$; $p < 0.01$) (Table 17).

The carbohydrate content marginally decreased from 6.0 % to 5.3 % in the control and to 5.7 % in the ablated lobsters (Fig. 27). The decrease was significantly different in the control ($f = 21.71$; $p < 0.01$) (Appendix 17a) and in the ablated ($f = 4.70$; $p < 0.01$) (Appendix 17b) lobsters. The amount of carbohydrate in the hepatopancreas, decreased from 94.9 mg/ 100g wet weight to 17.0 mg/ 100 g in the control (Table 18) and to 14.8 mg/ 100 g in the ablated lobsters (Table 19). The ANOCOVA showed no significant difference in the carbohydrate content between the control and ablated lobsters ($f = 0.45$; $p > 0.05$) (Table 17).

Table 18. Effect of starvation on the wet weight of hepatopancreas and on the quantitative changes in proximate composition (mg/100 g wet weight) and energy content (kj/100 g wet body weight) in the hepatopancreas of control *P. homarus*; ± indicates standard deviation

Weeks of starvation	Hepatopancreas (g)	Water	Protein	Lipid	Carbohydrate	Ash	Energy
0	4.52 ± 0.1	2901.8 ± 65.0	890.4 ± 18.5	542.4 ± 18.1	94.9 + 13.4	85.9 ± 12.1	41.6 ± 1.0
1	4.46 ± 0.1	2988.2 ± 61.0	794.9 ± 16.8	504.0 ± 17.8	93.7 ± 4.5	84.7 ± 4.0	37.7 ± 0.4
2	4.19 ± 0.3	2949.8 ± 5.9	645.3 ± 13.6	431.6 ± 12.6	83.8 ± 4.2	76.9 ± 4.0	31.5 + 0.6
3	4.15 ± 0.2	3012.9 ± 74.7	593.5 ± 12.5	390.1 ± 4.2	78.9 ± 4.2	78.9 ± 4.1	28.5 ± 0.1
6	2.69 ± 0.2	2036.3 ± 61.9	373.9 ± 6.0	193.7 ± 5.4	35.0 + 2.7	51.1 ± 3.9	15.7 ± 0.3
9	2.54 ± 0.1	1971.0 ± 29.3	350.5 ± 9.5	144.8 ± 5.1	22.9 ± 1.0	48.3 ± 1.3	13.1 ± 0.3
13	2.18	1789.8	242.0	87.2	19.6	41.4	8.5
14	2.15	1788.8	230.1	73.1	19.4	40.9	7.6
15	2.13	1795.6	217.3	59.6	17.0	40.5	6.8

Table 19. Effect of starvation on the wet weight of hepatopancreas and on the quantitative changes in proximate composition (mg/100 g wet weight) and energy content (kj/100 g wet body weight) in the hepatopancreas of ablated *P. homarus*; ± indicates standard deviation

Weeks of starvation	Hepatopancreas (g)	Water	Protein	Lipid	Carbohydrate	Ash	Energy
0	4.52 ± 0.1	2901.8 ± 65.0	890.4 ± 18.5	542.4 ± 18.1	94.9 ± 13.4	85.9 ± 12.1	41.6 ± 1.0
1	4.39 ± 0.4	2950.1 ± 60.2	785.8 ± 8.8	500.5 ± 17.5	70.2 ± 8.8	83.4 ± 8.7	37.0 ± 0.6
2	3.67 ± 0.2	2580.0 ± 29.5	601.9 ± 14.7	374.3 ± 18.3	47.7 ± 3.6	69.7 ± 3.6	27.7 ± 0.4
3	3.61 ± 0.1	2685.8 ± 50.5	498.2 ± 25.3	314.1 ± 10.8	46.9 ± 3.5	68.6 ± 3.6	22.9 ± 0.8
6	2.32 ± 0.1	1823.5 ± 46.4	309.9 ± 7.1	127.6 ± 4.6	23.2 ± 2.3	44.1 ± 2.3	11.4 ± 0.2
7	2.24 ± 0.1	1904.0 ± 24.6	221.8 ± 8.9	56.0 ± 2.2	17.9 ± 2.1	42.6 ± 4.4	6.7 ± 0.1
8	2.12	1857.1	171.7	36.0	14.8	40.3	4.8

Fig. 26. Effect of starvation on the lipid content in the hepatopancreas of *P. homarus*; the vertical lines indicate standard deviation

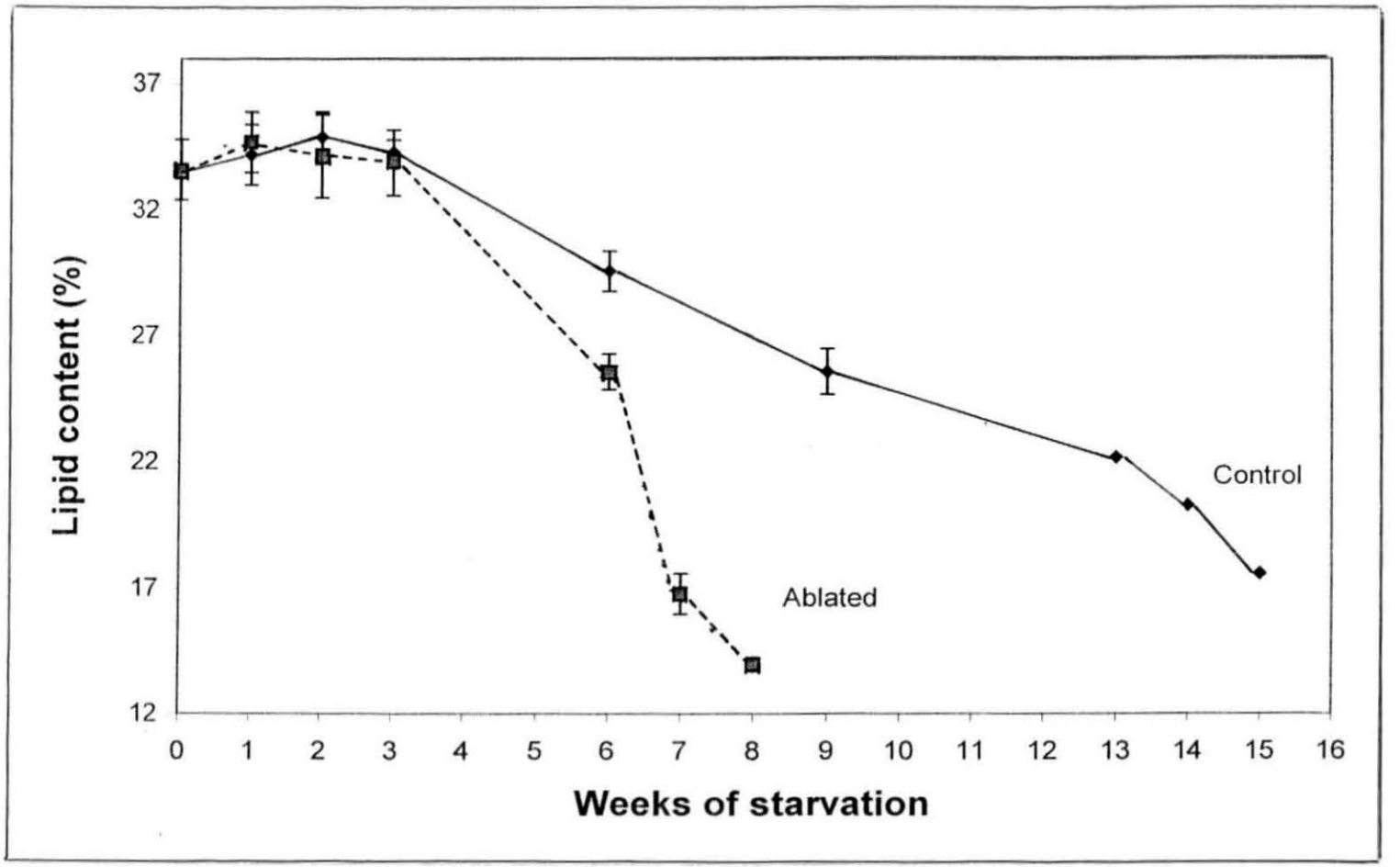
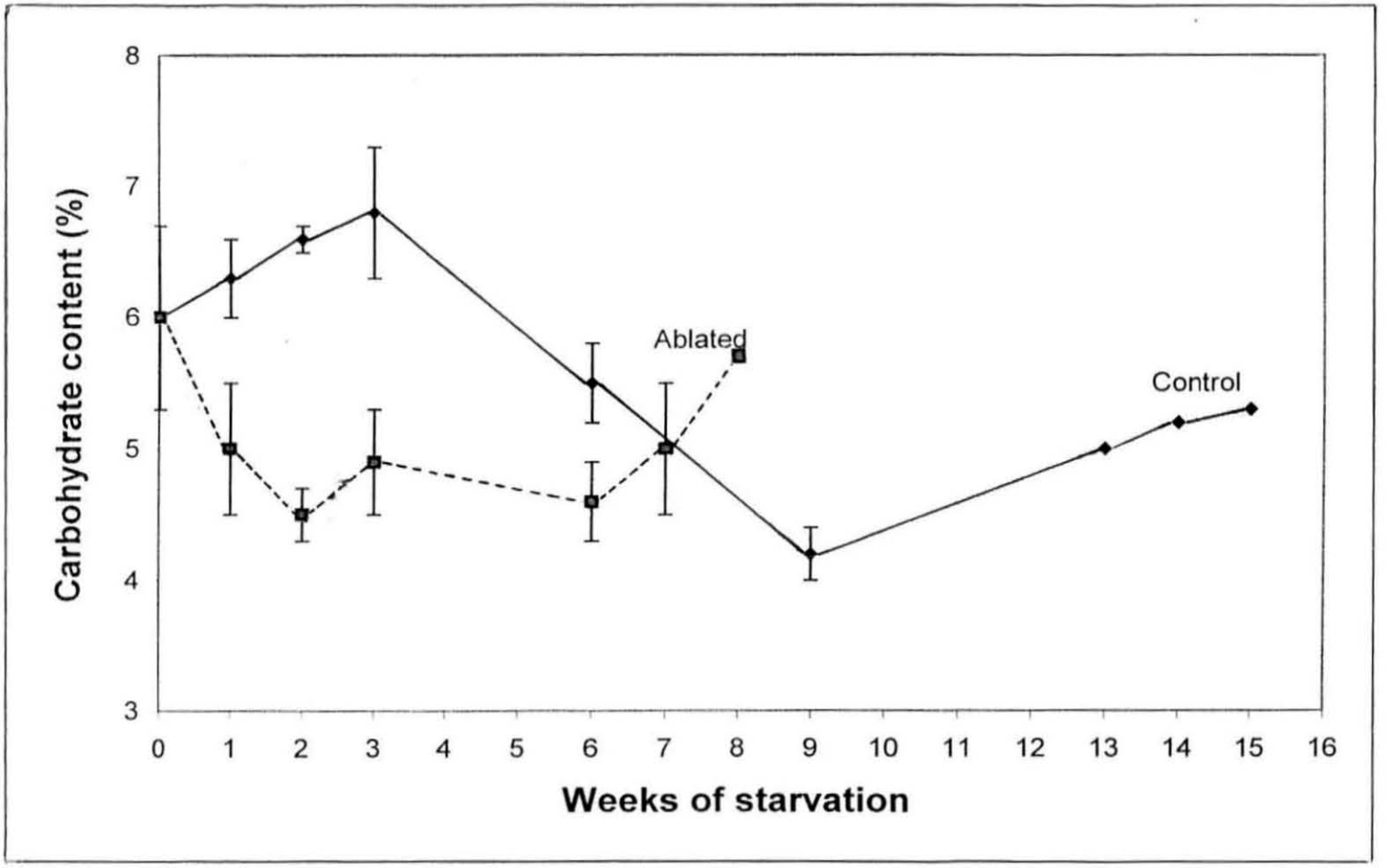


Fig. 27. Effect of starvation on the carbohydrate content in the hepatopancreas of *P. homarus*; the vertical lines indicate standard deviation



The ash content increased considerably from 5.2 % in the first day of starvation to 11.9 % in the 15 th week (Fig. 28) in the control and to 15.1 % in the 8 th week in the ablated lobsters (Fig. 28). The increase was 227 % for the control and 288 % for the ablated lobsters. The increase was significantly different in the control ($f = 65.20$; $p < 0.01$) (Appendix 18a) as well as in the ablated lobsters ($f = 106.31$; $p < 0.01$) (Appendix 18b). The ANOCOVA showed significant difference ($f = 80.29$; $p < 0.01$) (Table 17) in the ash content between the control and ablated lobsters.

The energy content decreased considerably in both the groups. It decreased from 25.7 kj/g to 20.3 kj/g in the control (Fig. 29) and to 18.4 kj/g in the ablated lobsters (Fig. 29). The decrease was highly significant in both the control ($f = 43.02$; $p < 0.01$) (Appendix 19a) as well as in the ablated ($f = 115.34$; $p < 0.01$) (Appendix 19b) lobsters. The rate of decrease in the energy content was maximum in the final phase of starvation in the ablated lobster. The ANOCOVA showed a significant difference in the energy content between the control and ablated lobsters ($f = 64.52$; $p < 0.01$) (Table 17).

4.2.5.3 Exoskeleton

The water content in the exoskeleton increased only marginally in both the control and ablated lobsters with the intensification of starvation. It increased from 36.4 % in the first day of starvation to 37.7 % in the control lobster (Fig. 30) after 15 weeks and to 37.8 % in the ablated lobster (Fig. 30) after 8 weeks of starvation. Both the groups of lobsters had equal water content upto 6 weeks and thereafter the ablated lobsters showed higher water content. The increase in the water content was not significant in both the control and ablated lobsters (Appendix 20a,b) and the difference in the water content between control and ablated lobsters was also statistically not significant (Table 17).

The decrease in the protein content was almost equal in the control and ablated lobsters. The decrease was from 3.6 % to 2.8 % in

Fig. 28. Effect of starvation on the ash content in the hepatopancreas of *P. homarus*; the vertical lines indicate standard deviation

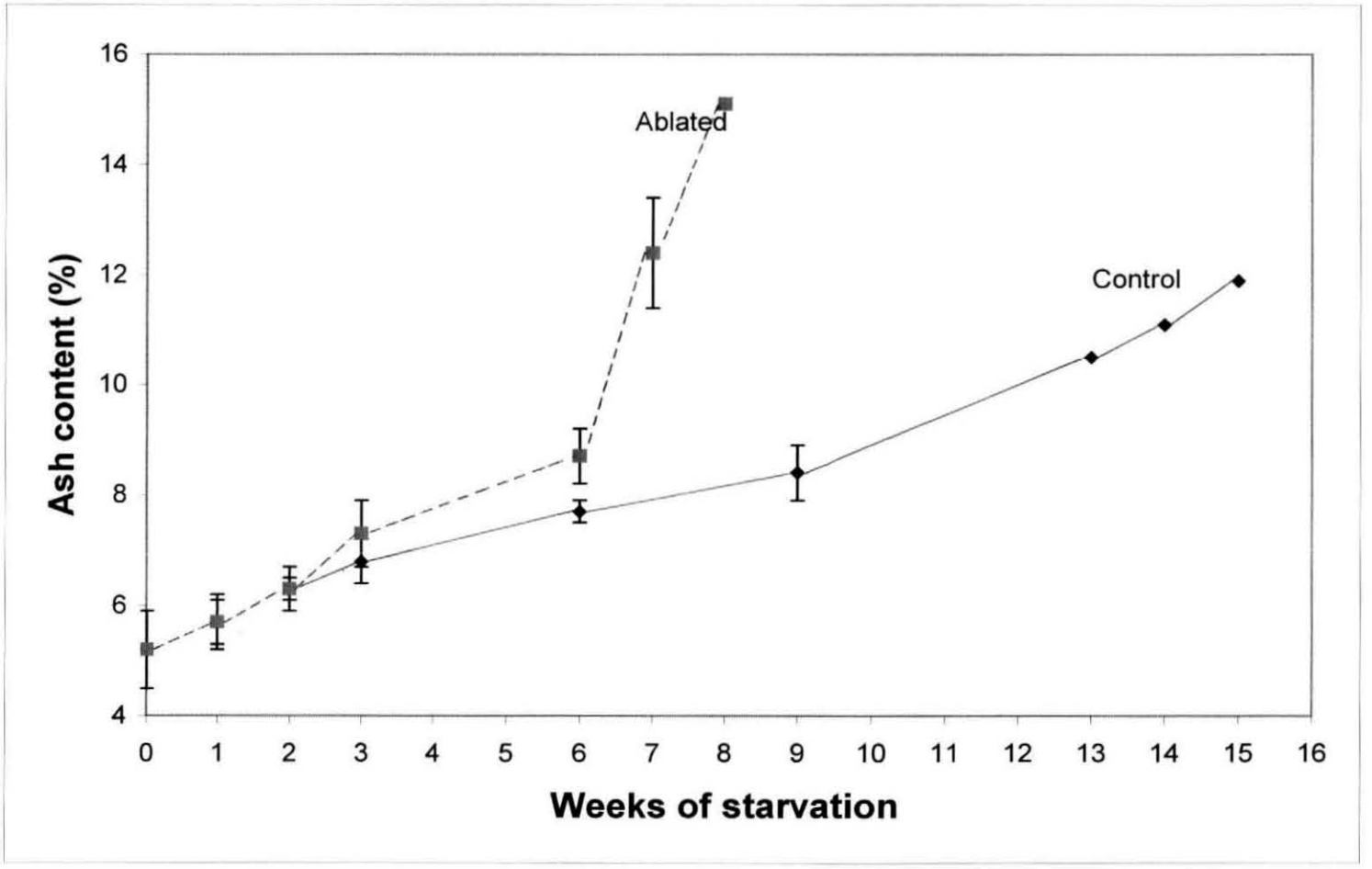


Fig. 29. Effect of starvation on the energycontent in the hepatopancreas of *P. homarus*; the vertical lines indicate standard deviation

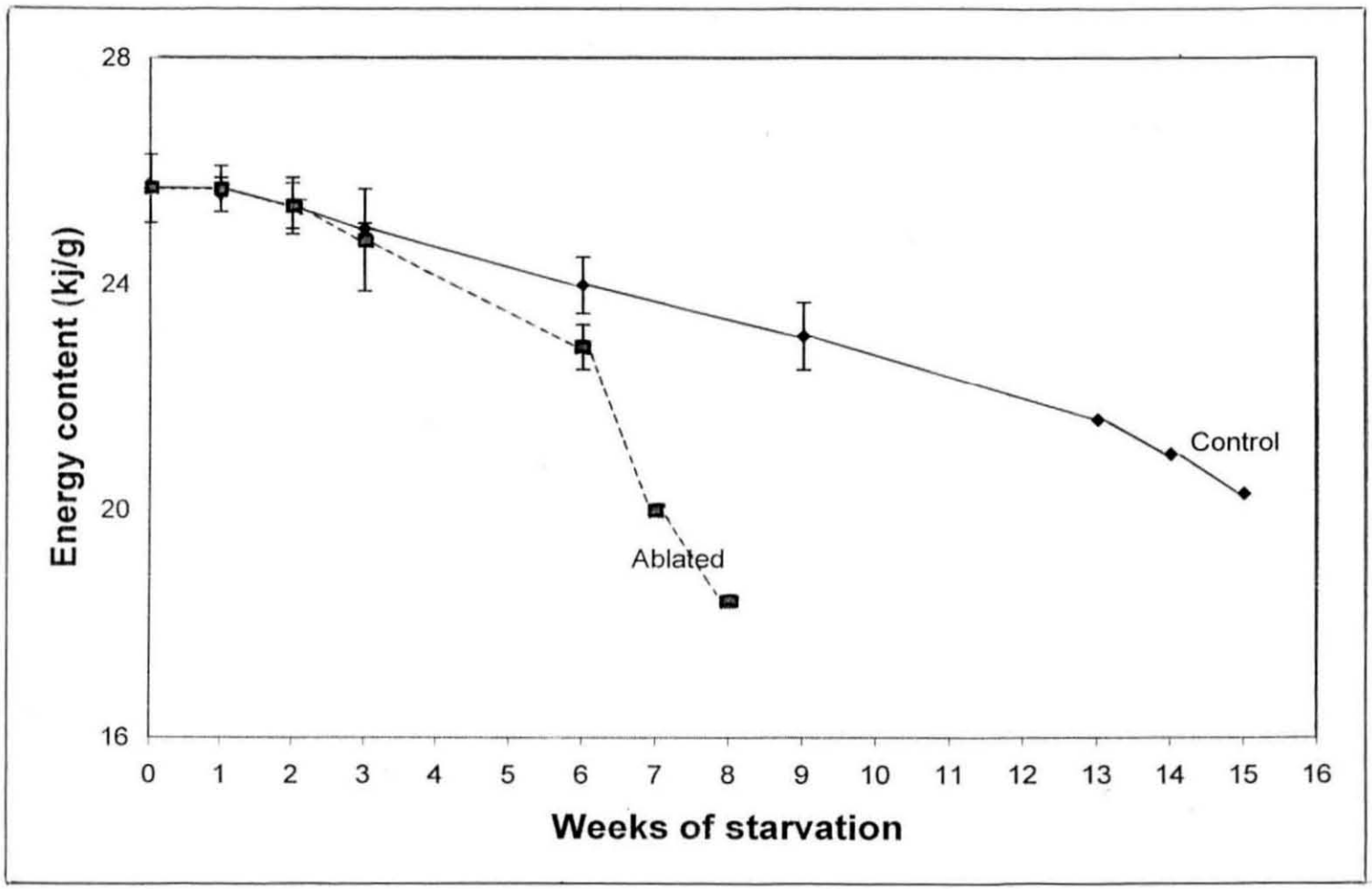
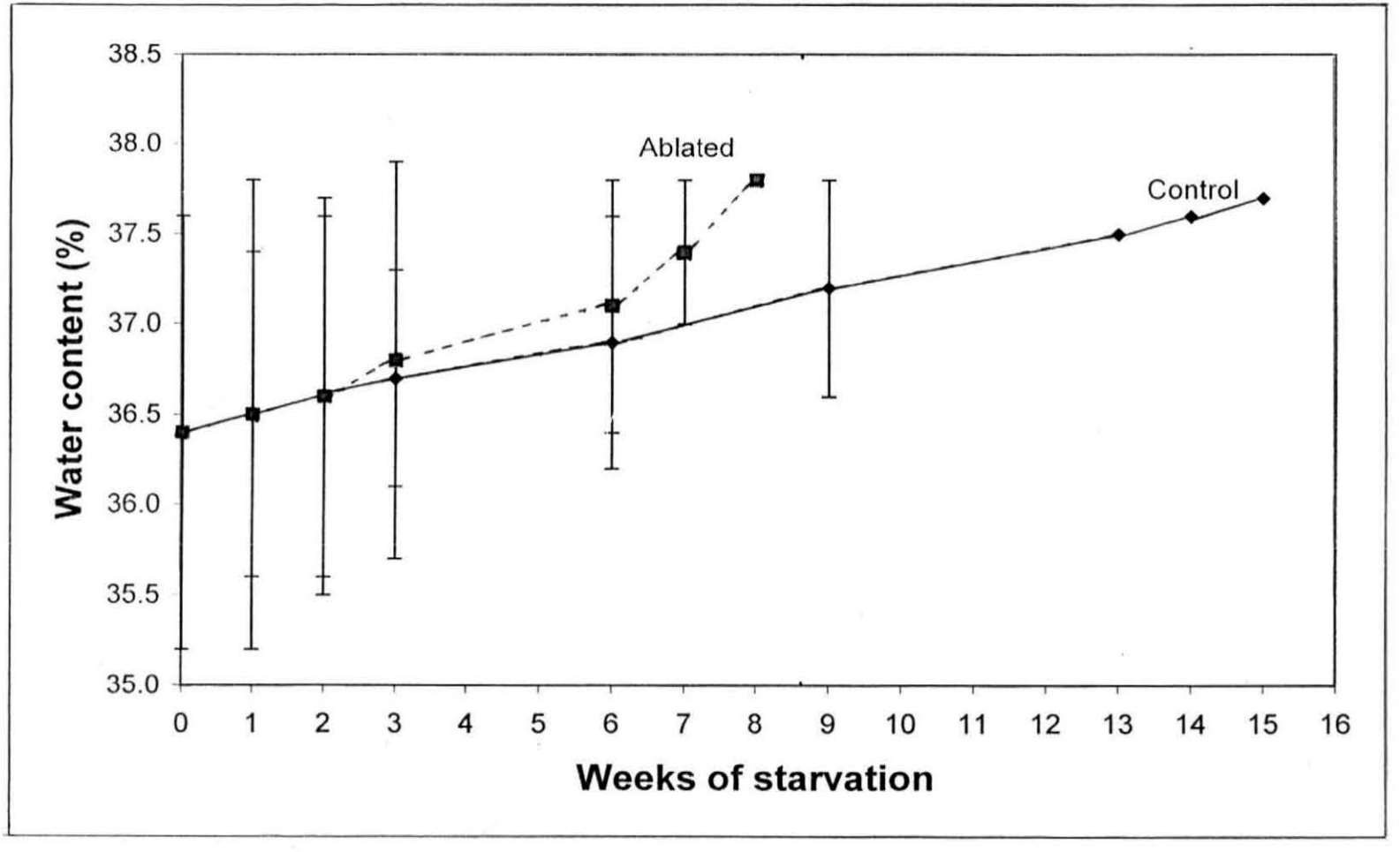


Fig. 30. Effect of starvation on the water content in the exoskeleton of *P. homarus*; the vertical line indicate standard deviation



the control (Fig. 31) and to 2.7 % in the ablated lobsters (Fig. 31). The decrease was highly significant in the control ($f = 36.63$; $p < 0.01$) (Appendix 21a) and in the ablated ($f = 52.35$; $p < 0.01$) (Appendix 21b) lobsters. The ANOCOVA showed no significant difference between the control and ablated lobsters ($f = 31.29$; $p < 0.01$) (Table 17).

The lipid content decreased from 0.9 % to 0.4 % in the control (Fig. 32) and to 0.3 % in the ablated lobsters (Fig. 32). The decrease was 60 % in the control and 65 % in the ablated lobsters. Significant difference in lipid content was observed in the control ($f = 35.21$; $p < 0.01$) (Appendix 22a) and in the ablated lobsters ($f = 42.47$; $p < 0.01$) (Appendix 22b). There was no significant difference between the control and ablated lobsters ($f = 41.72$; $p < 0.01$) (Table 17).

The carbohydrate content decreased in both the control and ablated lobsters (1.5 % to 1.0 %) (Fig. 33). The decrease was significant in both the control ($f = 19.21$; $p < 0.01$) (Appendix 23a) and ablated ($f = 9.96$; $p < 0.01$) (Appendix 23b) lobsters. Both the groups showed similar carbohydrate content upto 6 weeks of starvation. However, a sudden decline was observed in the ablated lobster after 6 weeks of starvation. The ANOCOVA showed significant difference between the control and ablated lobsters ($f = 91.42$; $p < 0.01$) (Table 17).

The ash content marginally increased from 94.0 % to 95.9 % in the control (Fig. 34) and to 96.1 % in the ablated lobsters (Fig. 34). The increase was not significant in both the groups (Appendix 24a, b). The difference in the ash content between the control and ablated lobsters was also not significantly different ($f = 0.96$; $p > 0.05$) (Table 17).

The energy content decreased from 0.08 kj/g to 0.03 kj/g in both the control and ablated lobsters (Fig. 35). The energy content was equal upto 3 weeks of starvation in both the groups, but thereafter declined rapidly in the ablated lobsters. The decrease in both the control ($f = 4.63$; $p < 0.01$) (Appendix 25a) and ablated ($f = 3.61$; $p < 0.05$) (Appendix 25b) lobsters was significant. The ANOCOVA showed

Fig. 31. Effect of starvation on the protein content in the exoskeleton of *P. homarus*; the vertical lines indicate standard deviation

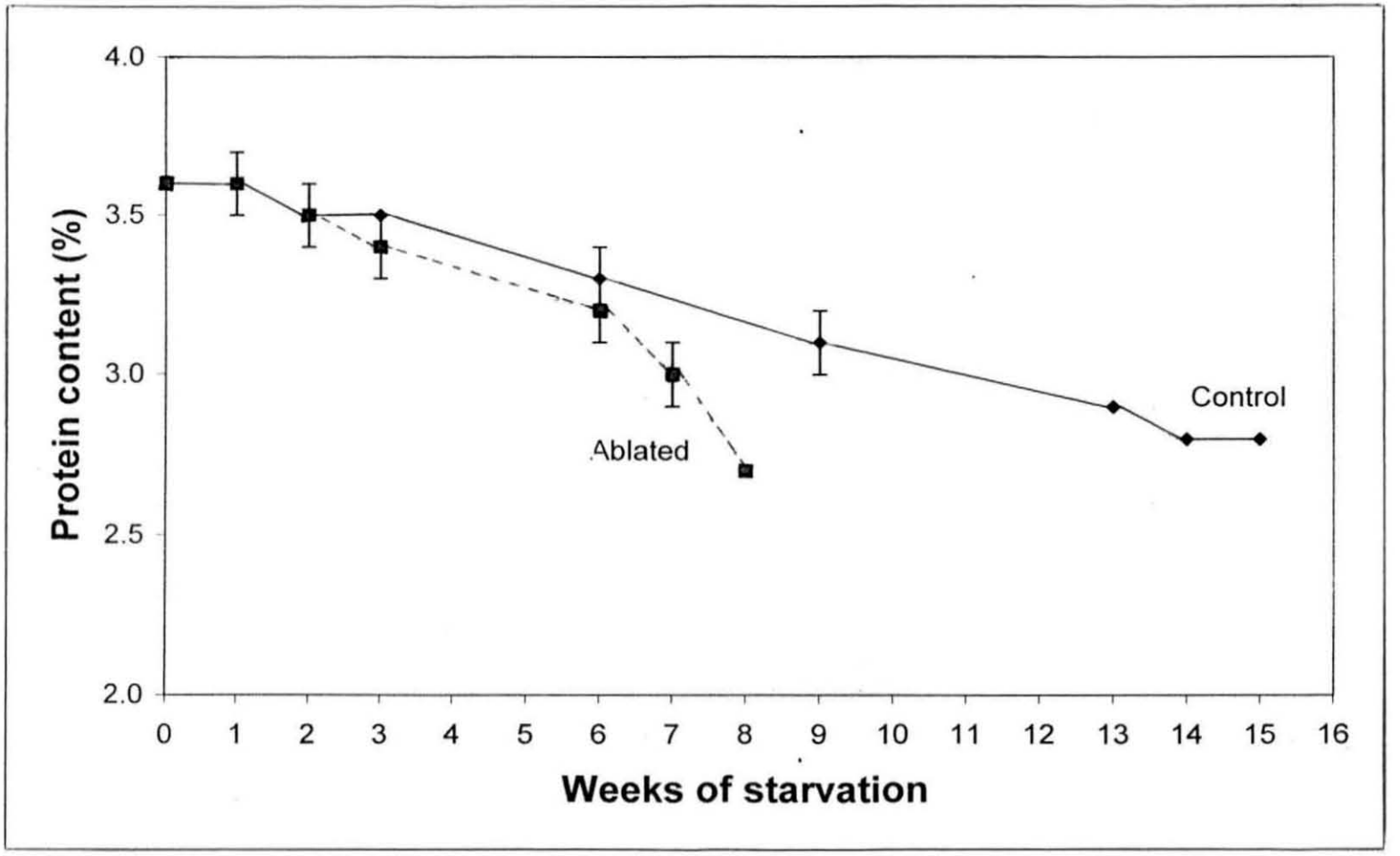


Fig. 32. Effect of starvation on the lipid content in the exoskeleton of *P. homarus*; the vertical lines indicate standard deviation

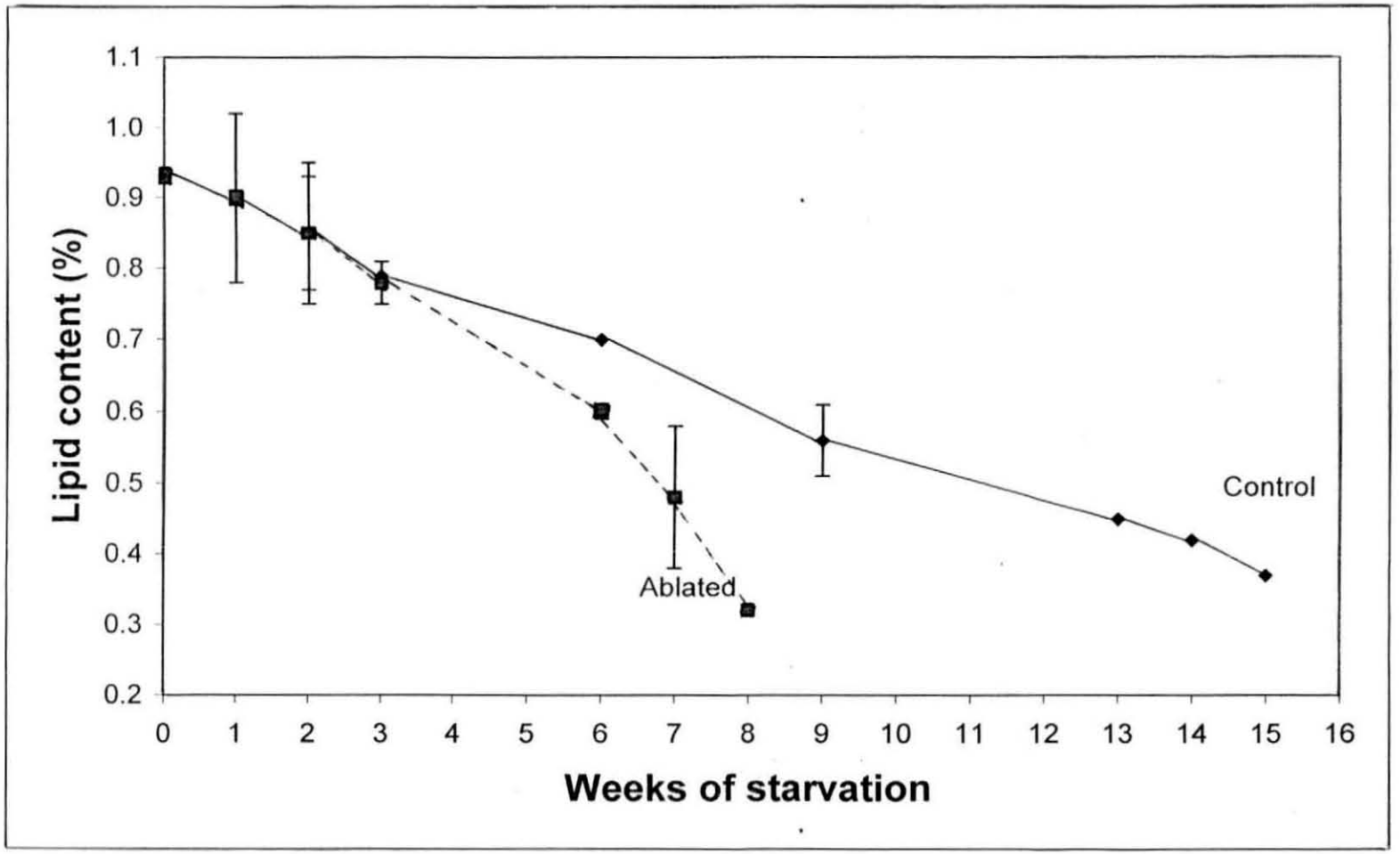


Fig. 33. Effect of starvation on the carbohydrate content in the exoskeleton of *P. homarus*; the vertical lines indicate standard deviation

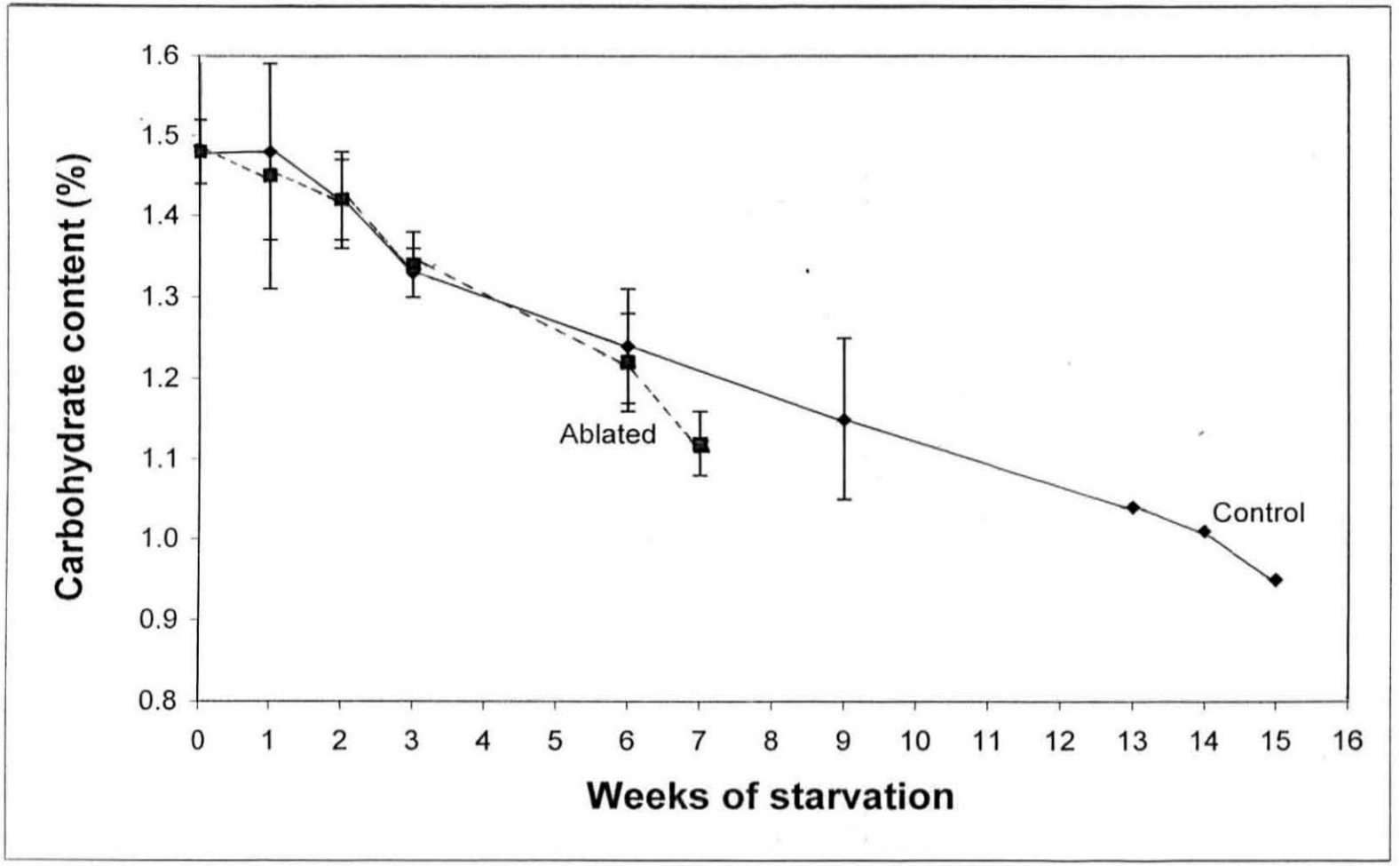


Fig. 34. Effect of starvation on the ash content in the exoskeleton of *P. homarus*; the vertical lines indicate standard deviation

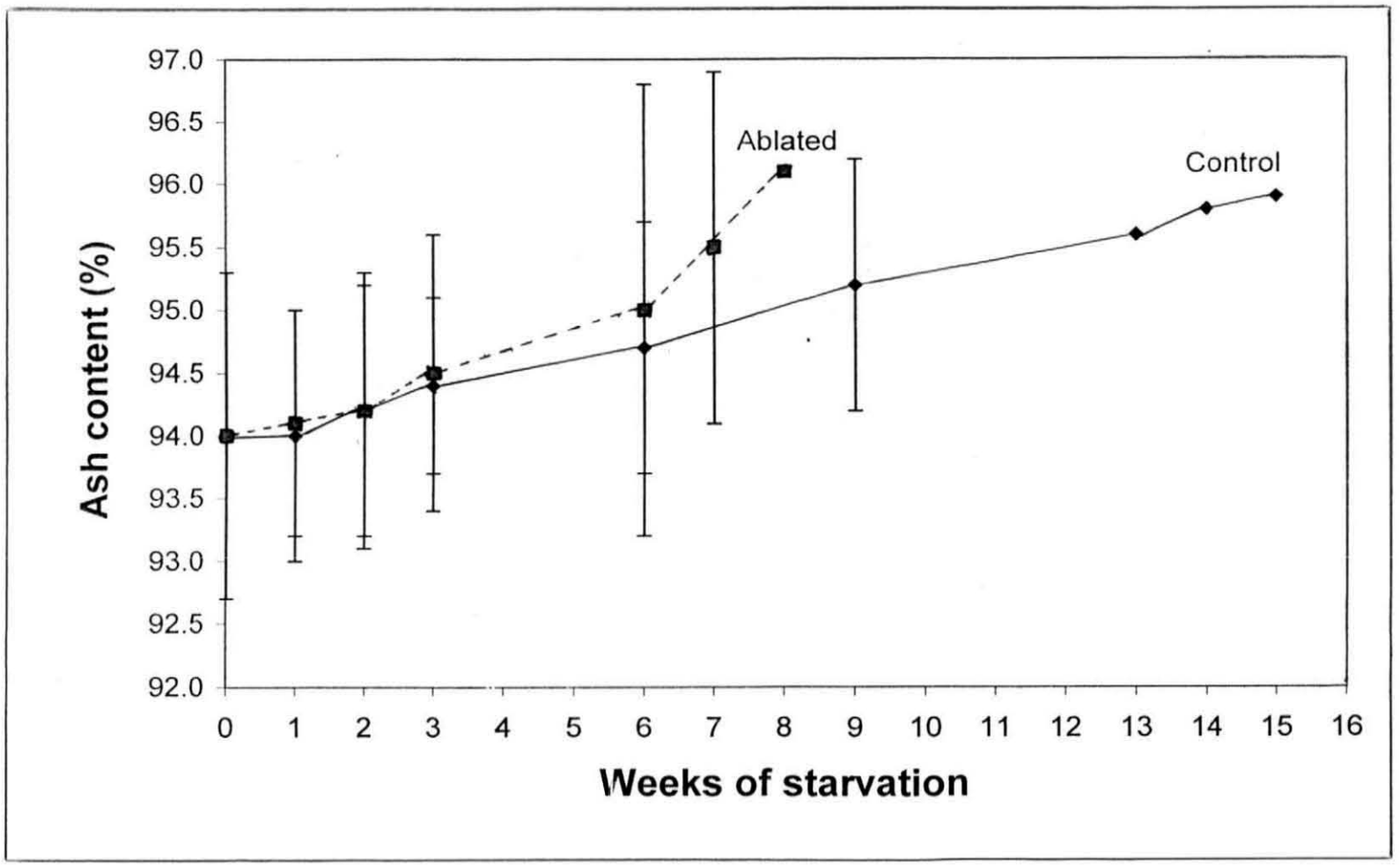
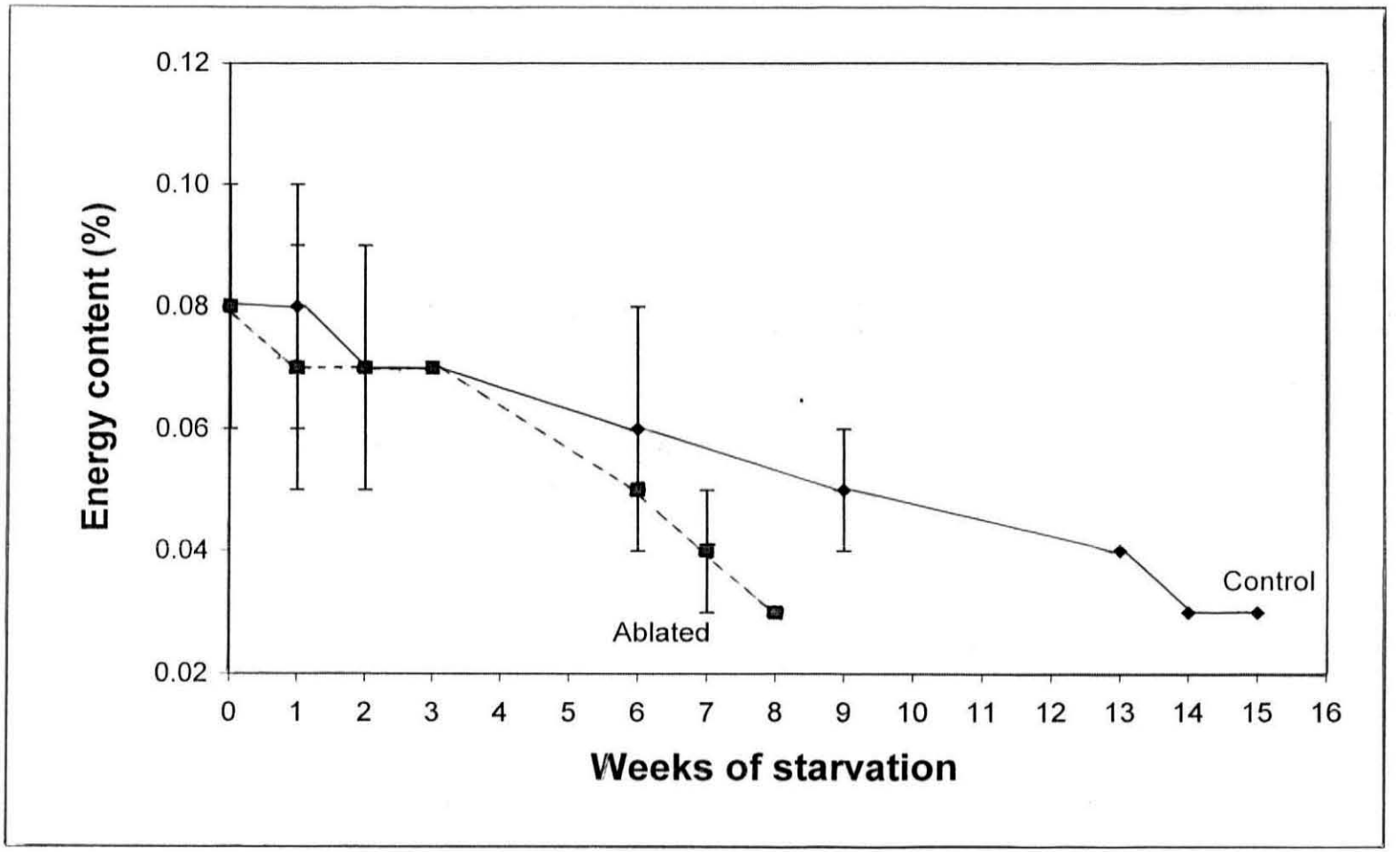


Fig. 35. Effect of starvation on the energy content in the exoskeleton of *P. homarus*; the vertical lines indicate standard deviation



significant difference in the energy content ($f = 4.52$; $p < 0.05$) (Table 17) between the control and ablated lobsters.

4.2.6 Protein-energy ratio

4.2.6.1 Tail muscle

The protein-energy ratio increased from 0.159 to 0.182 in the control and to 0.185 in the ablated lobsters (Fig. 36a). The decrease was significant in the control ($f = 77.32$; $p < 0.01$) (Appendix 26a) and in the ablated lobsters ($f = 113.38$; $p < 0.01$) (Appendix 26b). The difference in the ratio between the control and ablated lobsters was also significant ($f = 7.67$; $p < 0.01$).

4.2.6.2 Hepatopancreas

In the hepatopancreas too, the protein-energy ratio increased in the control (0.0898 to 0.1343) and in the ablated (0.0898 to 0.1479) lobsters (Fig. 36b). The decrease was significantly different in both the control ($f = 830.45$; $p < 0.01$) (Appendix 27a) and ablated ($f = 338.38$; $p < 0.01$) (Appendix 27b) lobsters. The difference in the ratio between the control and ablated lobsters was also significant ($f = 9.30$; $p < 0.01$).

4.2.6.3 Exoskeleton

It increased from 1.95 to 2.55 in the control and to 5.51 in the ablated lobsters (Fig. 36c). The difference in the ratio was not significantly different in the control ($f = 2.06$; $p > 0.05$) (Appendix 28a) and ablated lobsters ($f = 1.33$; $p > 0.05$) (Appendix 28b). The ratio between the control and ablated groups were also significantly different ($f = 16.58$; $p < 0.01$).

4.3 Effect of different food on food utilization

4.3.1 Food composition

The water, proximate and energy contents of various feeds used in the experiment are given in Table 20. The highest water content

Fig. 36 Effect of starvation on the protein-energy ratio in the tail muscle (a), hepatopancreas (b) and exoskeleton (c) of *P. homarus*; the vertical lines indicate standard deviation

Fig.36a

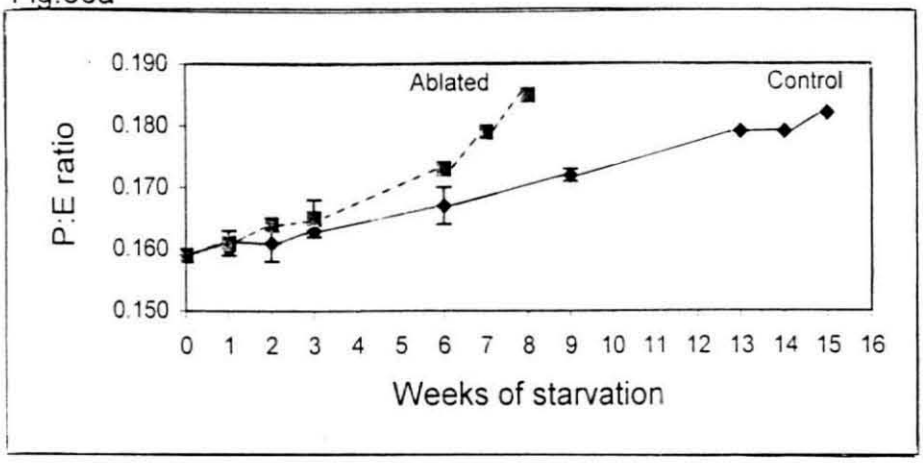


Fig. 36b

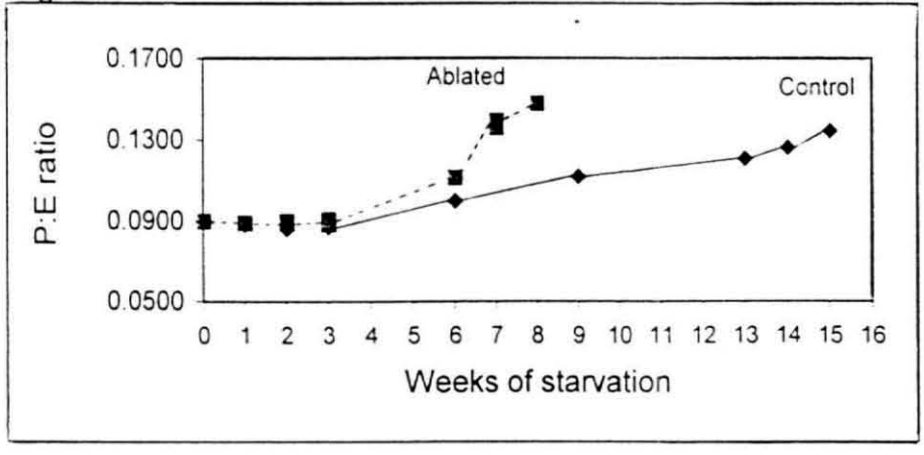


Fig. 36c

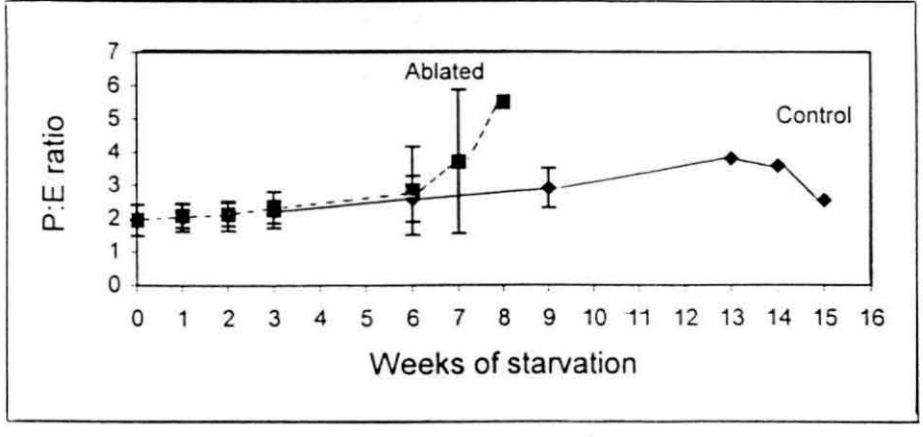


Table 20. Proximate composition and energy contents in various food items as percentage dry weight; ± indicates standard deviation

Parameter	Food			
	Shrimp	Squid	Clam	Mussel
Water content (%)	78.5 ± 0.7	80.0 ± 0.3	80.8 ± 1.1	77.1 ±1.0
Protein (%)	68.6 ± 0.9	68.2 ± 1.5	56.8 ±1.3	64.7 ± 1.4
Lipid (%)	8.8 ± 1.8	5.0 ± 0.7	7.6 ± 0.5	10.2 ± 1.1
Carbohydrate (%)	4.4 ± 0.8	12.9 ± 0.9	24.4 ± 1.4	13.13 ± 0.5
Ash (%)	18.1 ± 0.8	13.9 ± 1.6	11.2 ± 0.6	12.0 ± 0.5
Energy (kj/g)	16.2 ± 0.4	17.6 ± 0.3	17.9 ± 0.5	18.3 ± 0.7

was observed in the clam (80.8 ± 1.1 %), which and was significantly different ($t = 3.52$; $p < 0.05$) (Table 21) from the water content of the mussel (77.1 ± 1.0 %), which had the lowest water content among all the four feeds. The protein content was lowest in the clam (56.8 ± 1.3 %) and was significantly low ($t = 10.55$; $p < 0.01$) (Table 21) compared to the feed with the highest protein content *i.e.*, shrimp (68.6 ± 0.9 %). The lipid content ranged from 5.0 ± 0.7 % (squid) to 10.2 ± 1.1 % (mussel); the difference was significant ($t = 5.64$; $p < 0.01$) (Table 21). The clam had the highest carbohydrate content (24.4 ± 1.4 %), and the shrimp, the lowest (4.4 ± 0.8 %). A significant difference ($t = 17.54$; $p < 0.01$) (Table 21) was observed between the values of carbohydrate contents. Ash content varied between 18.1 ± 0.8 % (shrimp) and 11.2 ± 0.6 % (clam). The difference in the ash content between the shrimp and clam was also significant ($t = 9.76$; $p < 0.01$) (Table 21). A significant difference ($t = 3.68$; $p < 0.05$) (Table 21) was observed in the energy content between the highest (mussel: 18.3 ± 0.7 kj/g) and the lowest (shrimp: 16.2 ± 0.4 kj/g) values.

4.3.2 Feeding rate

The highest and lowest feeding rates were observed in *P. homarus* fed with mussel (263.45 ± 20.29 j/g/d) and squid (209.62 ± 20.68 j/g/d), respectively (Table 22). In other words, the lobster has the capacity to increase the feeding rate up to 25.7 % depending up on the food consumed. The highest and lowest feeding rates were significantly different ($t = 3.22$; $p < 0.05$) (Table 23).

4.3.3 Excretion

The energy loss through excretion ranged between 3.69 ± 0.46 j/g/day (squid-fed) and 8.43 ± 1.65 j/g/day (shrimp-fed). The faeces constituted 40.8% (clam-fed) to 50.0% (shrimp-fed) of the total excretion. Nitrogenous excretory product (ammonia) constituted the rest.

Table 21. Result of Student's t test between different food items

Parameter	Food	t - test	
		t - value	p - value
Water content	Clam / Mussel	3.52	< 0.05
Protein	Shrimp / Clam	0.55	< 0.01
Lipid	Mussel / Squid	5.64	< 0.01
Carbohydrate	Clam / Shrimp	17.54	< 0.01
Ash	Shrimp / Clam	9.76	< 0.01
Energy	Mussel / Shrimp	3.68	< 0.05

Table 22. Effect of different food on food utilization parameters of *P. homarus*; ± indicates standard deviation

Parameter	Feed			
	Shrimp	Squid	Clam	Mussel
Feeding rate (j/g/day)	251.57 ± 14.70	209.62 ± 20.68	235.57 ± 9.51	263.45 ± 20.29
Assimilation rate (j/g/day)	243.14 ± 15.08	205.94 ± 20.62	230.70 ± 10.38	256.94 ± 20.41
Assimilation efficiency (%)	96.65 ± 0.74	98.24 ± 0.25	97.93 ± 0.59	97.53 ± 0.38
Conversion rate (j/g/day)				
Exuvia (E)	8.16 ± 0.09	8.19 ± 0.32	8.55 ± 0.07	8.58 ± 0.12
Growth (P)	21.27 ± 0.59	14.55 ± 1.50	23.86 ± 0.98	20.76 ± 1.31
P+E	29.43 ± 0.53	22.74 ± 1.19	32.41 ± 0.92	29.34 ± 1.35
Metabolic rate				
j/g/day	213.67 ± 14.59	183.20 ± 19.46	198.29 ± 10.53	227.60 ± 19.45
ml O_2/ g/hr	0.45 ± 0.03	0.38 ± 0.04	0.41 ± 0.03	0.47 ± 0.04
Conversion efficiency (K_2) (%)				
Exuvia (E)	3.41 ± 0.29	4.01 ± 0.55	3.71 ± 0.18	3.35 ± 0.30
Growth (P)	8.86 ± 0.44	7.06 ± 0.12	10.36 ± 0.67	8.09 ± 0.40
E + P	12.26 ± 0.73	11.08 ± 0.54	14.07 ± 0.80	11.45 ± 0.66

Table 23. Result of the Student's t test for food utilization parameters of *P. homarus* fed with different food items

Parameter	Feeds	t test	
		t - value	p - value
Feeding rate	Mussel/ Squid	3.22	< 0.05
Assimilation rate	Mussel/ Squid	3.53	< 0.05
Conversion rate			
P + E	Clam/ Squid	9.00	< 0.01
E	Mussel/ Shrimp	4.85	< 0.01
P	Clam/ Squid	11.14	< 0.01
Metabolic rate	Mussel/ Squid	2.80	< 0.05

4.3.4 Rate and efficiency of assimilation

Assimilation efficiency was very high in all the groups (Table 22), ranging from 96.7 % to 98.2 %. Assimilation rate ranged from 205.9 ± 20.6 j/g/d (squid-fed) to 256.9 ± 20.4 j/g/d (mussel-fed). The difference between the highest and lowest assimilation rate was significant ($t = 3.53$; $p < 0.05$).

4.3.5 Metabolic rate

The metabolic rate was highest in the group receiving mussels (227.6 ± 19.5 j/g/d or 0.47 ± 0.04 ml O_2/g live weight/h) and the lowest in the squid-fed group (183.2 ± 19.5 j/g/d or 0.38 ± 0.04 ml O_2/g /h) (Table 22). The difference between the highest and lowest metabolic rates was significant ($t = 2.80$; $p < 0.05$) (Table 23). The metabolic rate was directly proportional to the feeding rate.

4.3.6 Moulting

During the 105 days experiment, all the lobsters moulted twice. The lobsters, which were in the intermoult stage (C stage) at the commencement of the experiment, completed the first moult in 30-38 days of the experiment. The intermoult duration between the first and second moults was longer for the lobsters fed on squid (52.3 ± 2.5 days) compared to the lobsters fed on clam (42.7 ± 1.5 days) (Fig. 37). Lobsters feeding on the mussel lost more wet weight as moult (53.4 ± 0.02 % of mid-body weight) compared to those feeding on shrimp (50.4 ± 1.4 % of the mid-body weight) (Fig. 38).

4.3.7 Weight increase

Live weight increase excluding moult was maximum in the lobsters fed with clam (66.0 ± 3.2 g) and minimum in the squid-fed lobsters (33.9 ± 0.9 g) (Table 24). The difference in the live weight gain was significant ($t = 16.73$; $p < 0.01$). The average daily wet weight gain ranged from 323.2 ± 8.2 mg/day in the squid-fed lobsters to 628.3 ± 30.7 mg/day in the clam-fed lobsters (Fig. 39). The total live weight gain

Fig. 37. Effect of different food items on the intermoult duration in *P. homarus*

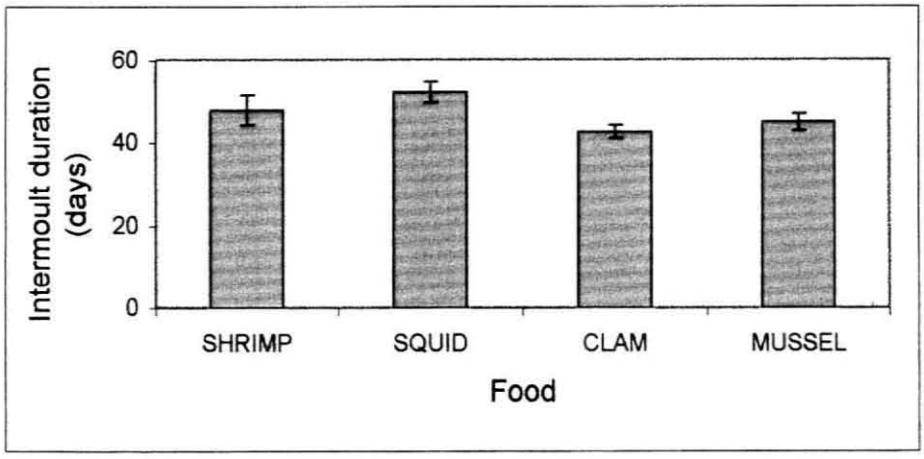


Fig. 38. Weight loss (% mid-body weight) as moult in *P. homarus* fed with different food items

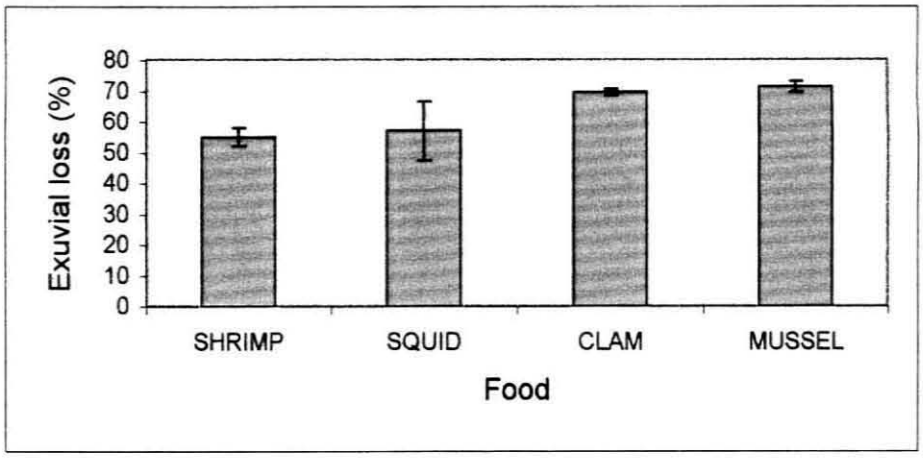


Fig. 39. Growth (g wet weight/ day) rate in *P. homarus* fed with different food items

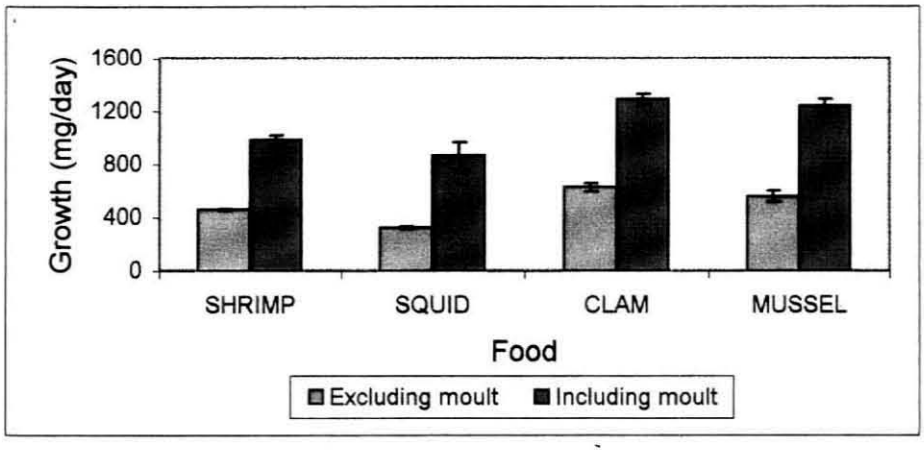


Table 24. Weight increase in *P. homarus* fed with different food items; ± indicates standard deviation

Parameter	Food			
	Shrimp	Squid	Clam	Mussel
Initial live weight (g)	83.6 ± 3.8	94.4 ± 14.0	97.8 ± 2.2	104.4 ± 3.2
Final live weight (g)	132.1 ± 4.4	128.3 ± 14.8	163.8 ± 3.8	163.0 ± 5.3
Live weight increase (g)	48.5 ± 0.8	33.9 ± 0.9	66.0 ± 3.2	58.6 ± 4.3
Exuvia weight (g)	55.1 ± 2.9	57.1 ± 9.5	69.6 ± 1.1	71.4 ± 1.8
Live weight increase including exuvia (g)	103.6 ± 3.5	91.0 ± 10.3	135.6 ± 3.8	130.0 ± 5.6

including the moult were 135.6 ± 3.8 g and 91.0 ± 10.3 g for the clam-fed and squid-fed lobsters, respectively (Table 24). The difference in the weight gain was significant ($t = 7.04$; $p < 0.01$). The rate of live weight gain ranged from 867.3 ± 98.3 mg/day (squid-fed) to 1290.9 ± 36.3 mg/day (clam-fed) (Fig. 39).

4.3.8 Rate and efficiency of conversion

Conversion rate excluding the moult was highest in the lobsters fed with clam (23.9 j/g/day) and lowest in the squid-fed lobsters (14.6 j/g/day) (Table 22); the highest and lowest values were significantly different ($t = 9.00$; $p < 0.01$) (Table 23). The gross (K_1) and the net (K_2) conversion efficiencies were 10.2 ± 0.7 % and 10.4 ± 0.7 % for the clam - fed and 6.9 ± 0.1 % and 7.1 ± 0.1 % for the squid-fed lobsters, respectively (Table 22).

Energy used for production of moult was maximum in the mussel-fed lobsters (8.6 ± 0.1 j/g/day) and minimum in the shrimp-fed lobsters (8.2 ± 0.1 j/g/day) (Table 22); the difference between the lowest and highest values was significant ($t = 4.85$; $p < 0.01$) (Table 23).

The conversion rate including the moult was highest in the lobsters fed with clam (32.4 ± 0.9 j/g/day) and the lowest in the squid-fed lobsters (22.7 ± 1.2 j/g/day) (Table 22); the highest and lowest values were significantly different ($t = 11.14$; $p < 0.01$) (Table 23). The gross (K_1) and net (K_2) conversion efficiencies were 13.8 ± 0.8 % and 14.1 ± 0.8% for the clam-fed and 10.9 ± 0.5 % and 11.1 ± 0.5 % for the squid-fed lobsters, respectively (Table 22).

4.3.9 Energy budget

The energy budget was constructed for *P. homarus* by partitioning the energy towards the processes related to the body functions and body structures and was calculated as percentage of energy consumed by the lobster. The different components of the energy budget are plotted in Fig. 40.

Fig. 40 Energy budget for *P. homarus* fed with different food

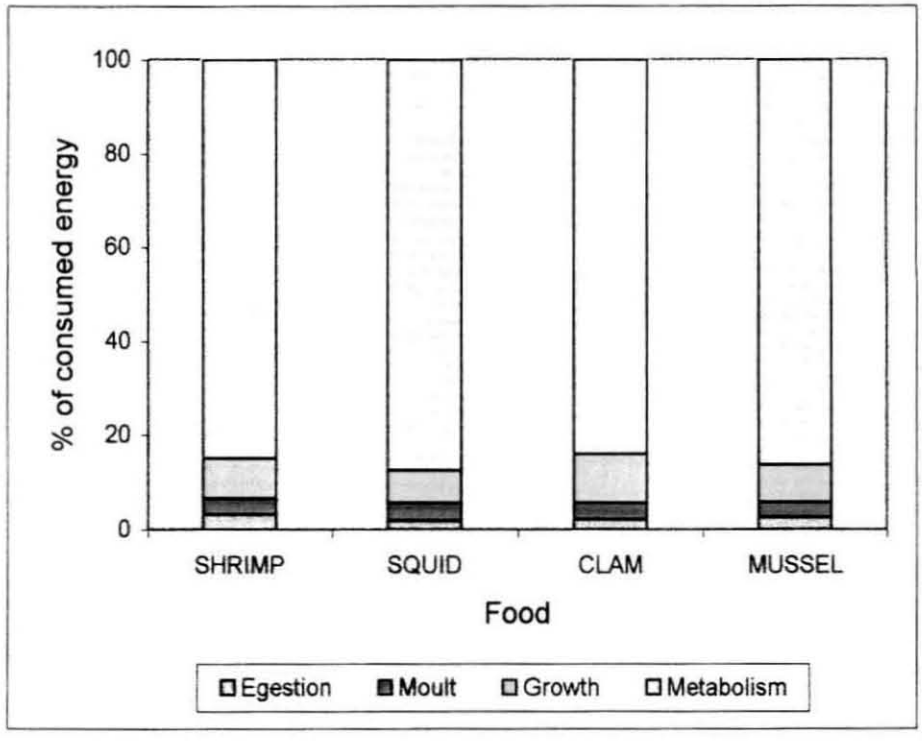
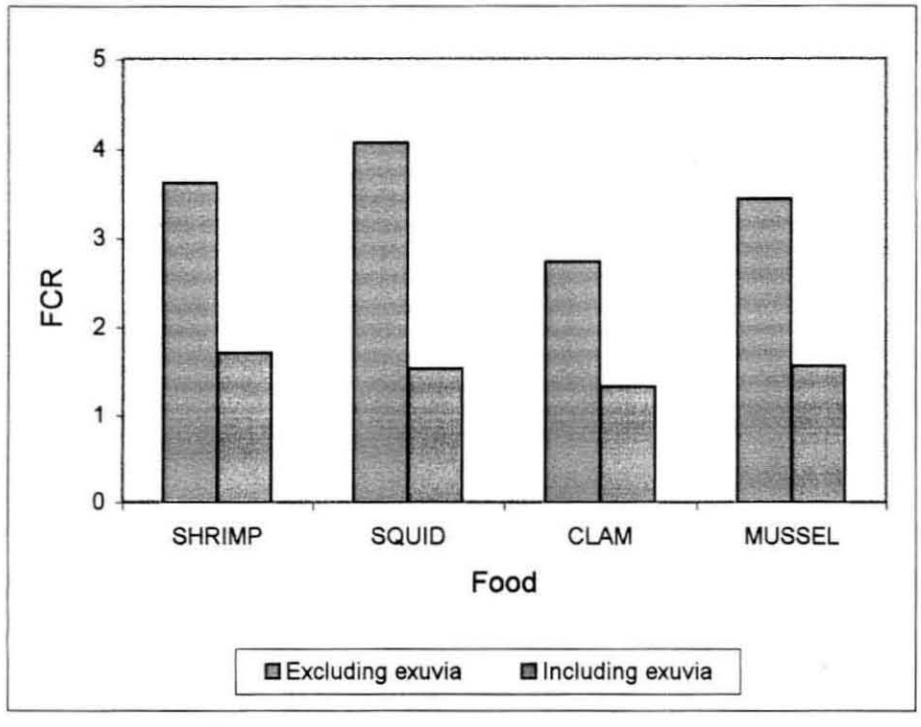


Fig. 41 Food conversion ratio (FCR) in *P. homarus* fed with different food



The lobsters spent 84.1 to 87.4 % of the consumed energy on metabolism. Energy loss through excretion ranged from 1.8 to 3.3 % of the consumed energy. Energy utilized for production including moult ranged from 10.9 to 13.8 % of the consumed energy, and 6.9 to 10.2 % of the consumed energy was used for actual production (excluding moult). Energy utilized for production of moult varied from 3.3 to 3.9 % of the consumed energy.

4.3.10 Proximate composition and energy contents of lobster

4.3.10.1 Water Content

The water content ranged between 74.5 to 75.3 % in the muscle, 60.7 to 63.6 % in the hepatopancreas, and 36.7 to 38.5 % in the exoskeleton at the end of the experiment (Table 25). The difference in the water content in the muscle and exoskeleton of lobsters fed with different food was not significant, whereas a significant difference was observed in the water content of the hepatopancreas (Table 26). In all the tissues, the lowest water content was observed in the clam-fed lobsters, whereas the squid-fed lobsters showed the highest water content in the muscle and hepatopancreas. However, irrespective of the food, the mean water content between the muscle (74.9 $\pm$ 0.4%), hepatopancreas (62.4 $\pm$ 1.2%) and exoskeleton (37.7 $\pm$ 0.9%) differed widely. Similar trend was observed in *P. homarus* collected from the wild (4.4.6.1; Table 13).

4.3.10.2 Protein

At the end of the experiment, the protein content in the muscle (78.5 to 79.6 % of dry weight), hepatopancreas (52.4 to 54.0 % of dry weight) and exoskeleton (3.3 to 3.6 % of dry weight) varied between lobsters, which received different food (Table 25); but the values were not significantly different (Table 26). The higher protein content in the muscle and exoskeleton of the shrimp-fed lobsters were in accordance with the higher protein content in the shrimp; in spite of this, the protein content in the hepatopancreas was lowest in the shrimp-fed lobsters.

Table 25. Proximate composition (% dry weight) and energy (kj/g) content in the tail muscle (25a), hepatopancreas (25b), and exoskeleton (25c) of *P. homarus* fed with different food items; ± indicates standard deviation

Table 25a

Feed	Water	Protein	Lipid	Carbohydrate	Ash	Energy
Control	77.55 ± 1.3	80.1 ± 1.0	10.4 ± 0.7	2.0 ± 0.1	7.4 ± 0.7	21.1 ± 0.3
Shrimp	75.0 ± 1.2	78.5 ± 1.2	10.9 ± 0.5	1.7 ± 0.1	8.9 ± 0.6	20.7 ± 0.1
Squid	75.3 ± 0.9	78.6 ± 1.4	10.8 ± 0.6	1.8 ± 0.1	8.8 ± 0.7	20.6 ± 0.2
Clam	74.5 ± 1.3	79.2 ± 1.5	11.3 ± 0.6	2.1 ± 0.1	7.4 ± 0.5	21.2 ± 0.5
Mussel	74.6 ± 1.1	79.6 ± 1.7	11.7 ± 0.6	2.0 ± 0.1	6.8 ± 0.6	21.6 ± 0.4

Table 25b

Feed	Water	Protein	Lipid	Carbohydrate	Ash	Energy
Control	65.7 ± 0.8	55.9 ± 1.4	33.0 ± 2.2	5.3 ± 0.4	5.8 ± 0.4	25.3 ± 1.0
Shrimp	62.4 ± 1.7	53.5 ± 0.9	34.6 ± 1.9	5.2 ± 0.4	6.6 ± 0.8	25.3 ± 0.8
Squid	63.6 ± 1.8	54.0 ± 1.3	34.1 ± 1.9	5.1 ± 0.4	6.8 ± 0.4	25.0 ± 1.0
Clam	60.7 ± 0.9	52.5 ± 1.0	35.5 ± 1.4	5.9 ± 0.5	6.2 ± 0.6	25.6 ± 0.6
Mussel	62.8 ± 2.1	52.4 ± 1.5	35.8 ± 1.7	5.8 ± 0.6	6.0 ± 0.7	25.7 ± 0.9

Table 25c

Feed	Water	Protein	Lipid	Carbohydrate	Ash	Energy
Control	39.9 ± 1.2	3.9 ± 0.2	1.3 ± 0.1	1.5 ± 0.1	93.3 ± 0.7	0.10 ± 0.01
Shrimp	38.5 ± 1.4	3.3 ± 0.3	1.4 ± 0.1	1.7 ± 0.1	93.5 ± 0.4	0.10 ± 0.02
Squid	38.3 ± 1.7	3.4 ± 0.2	1.4 ± 0.1	1.6 ± 0.1	93.6 ± 1.0	0.10 ± 0.01
Clam	36.7 ± 1.2	3.5 ± 0.3	1.6 ± 0.0	2.2 ± 0.2	92.7 ± 0.8	0.14 ± 0.01
Mussel	37.1 ± 1.7	3.6 ± 0.2	1.9 ± 0.1	1.9 ± 0.1	92.7 ± 1.0	0.14 ± 0.02

Table 26. Result of analysis of Student's t test for proximate composition and energy contents in various tissues of *P. homarus* fed with different food

Parameter	Feeds	t- test	
		t - value	p - value
Water content			
Muscle	Squid / Clam	0.88	> 0.05
Hepatopancreas	Squid / Clam	2.50	< 0.05
Exoskeleton	Shrimp / Clam	1.69	> 0.05
Protein			
Muscle	Mussle / Shrimp	0.92	> 0.05
Hepatopancreas	Squid / Mussel	1.40	> 0.05
Exoskeleton	Mussel / Shrimp	1.44	> 0.05
Lipid			
Muscle	Mussle / Squid	1.84	> 0.05
Hepatopancreas	Mussle / Squid	1.16	> 0.05
Exoskeleton	Mussle / Squid / Shrimp	6.12	< 0.01
Carbohydrate			
Muscle	Clam / Shrimp	4.90	< 0.01
Hepatopancreas	Clam / Squid	2.16	> 0.05
Exoskeleton	Clam / Squid	4.65	< 0.01
Ash			
Muscle	Shrimp / Mussel	4.29	< 0.01
Hepatopancreas	Squid / Mussel	1.72	> 0.05
Exoskeleton	Squid / Clam / Mussel	1.10	> 0.05
Energy			
Muscle	Mussel / Squid	3.87	< 0.01
Hepatopancreas	Mussel / Squid	0.90	> 0.05
Exoskeleton	Mussel / Clam / Shrimp / Squid	2.45	= 0.05

However, irrespective of the food, the mean protein content between the muscle (79.0 ± 0.5 % of dry weight), hepatopancreas (53.1 ± 0.8 % of dry weight) and exoskeleton (3.5 ± 0.1 % of dry weight) differed widely. Similar trend was observed in *P. homarus* collected from the wild (4.1.6.2; Table 13).

4.3.10.3 Lipid

At the end of the experiment, the lipid content in the muscle (10.8 to 11.7 % of dry weight), hepatopancreas (34.1 to 35.8 % of dry weight) and exoskeleton (1.4 to 1.9 % of dry weight) varied between lobsters, which received different food (Table 25) but the values were not significantly different in the muscle and hepatopancreas, whereas, the values were significantly different in the exoskeleton (Table 26). The lipid content in the tissues examined changed in accordance to the lipid content in the food. However, irrespective of the food, the mean lipid content between the muscle (11.2 ± 0.4 % of dry weight), hepatopancreas (35.0 ± 0.8 % of dry weight) and exoskeleton (1.6 ± 0.2 % of dry weight) differed widely. Similar trend was observed in *P. homarus* collected from the wild (4.4.6.3; Table 13).

4.3.10.4 Carbohydrate

At the end of the experiment, the carbohydrate content in the muscle (1.7 to 2.1 % of dry weight), hepatopancreas (5.1 to 5.9 % of dry weight) and exoskeleton (1.6 to 2.2 % of dry weight) varied between the lobsters, which received different food (Table 25). The values were significantly different in the muscle and exoskeleton, whereas, the values were not significantly different in the hepatopancreas (Table 26). The high carbohydrate content in the clam has been expressed in all the tissues of the lobster fed with clam. However, irrespective of the food, the mean carbohydrate content between the muscle (1.9 ± 0.2 % of dry weight), hepatopancreas (5.5 ± 0.4 % of dry weight) and exoskeleton (1.9 ± 0.3 % of dry weight) differed widely. Similar trend was observed in *P. homarus* collected from the wild (4.1.6.4; Table 13).

4.3.10.5 Ash

At the end of the experiment, the ash content in the tail muscle (6.8 to 8.9 % of dry weight), hepatopancreas (6.0 to 6.8 % of dry weight) and exoskeleton (92.7 to 93.6 % of dry weight) varied between the lobsters, which received different food (Table 25) but the values were not significantly different in the hepatopancreas and exoskeleton, whereas, the values were significantly different in the muscle (Table 26). The group fed with mussel showed constantly low ash content in the tissues examined. However, irrespective of the food, the mean ash content between the muscle (8.0 $\pm$ 1.0 % of dry weight), hepatopancreas (6.4 $\pm$ 0.4 % of dry weight) and exoskeleton (93.1 $\pm$ 0.5 % of dry weight) differed widely. Similar trend was observed in *P. homarus* collected from the wild (4.1.6.5; Table 13).

4.3.10.6 Energy Content

At the end of the experiment, the energy content in the tail muscle (20.6 to 21.6 kj/g), hepatopancreas (25.0 to 25.7 kj/g) and exoskeleton (0.10 to 0.14 kj/g) varied between lobsters, which received different food (Table 25). The values were significantly different in the muscle and exoskeleton, whereas, the values were not significantly different in the hepatopancreas (Table 26). The mussel-fed and clam-fed lobsters showed higher energy content in the tissues than the initial values. The tissues of the group fed with squid had the lowest energy content than that of the other groups. However, irrespective of the food, the mean energy content between the muscle (21.0 $\pm$ 0.3 kj/g), hepatopancreas (25.4 $\pm$ 0.3 kj/g) and exoskeleton (0.12$\pm$ 0.02 kj/g) differed widely. Similar trend was observed in *P. homarus* collected from the wild (4.1.6.6; Table 13).

4.3.11 Food Conversion Ratio (FCR)

The Food Conversion Ratio (FCR) for growth (P) ranged between 2.74 $\pm$ 0.17 (clam-fed lobsters) and 4.08 $\pm$ 0.06 (squid-fed lobsters), and including moult, the FCR reduced to 1.33 $\pm$ 0.06 (clam-fed

lobsters) and 1.53 ± 0.13 (squid-fed lobsters), respectively (Fig. 41). When moult was considered as growth, the FCR of the shrimp-fed (1.71 ± 0.09) and mussel-fed lobsters (1.56 ± 0.09) were more than that of the squid-fed lobsters (which had the highest FCR when only increase in live body weight was considered), indicating that the production of moult was more in the shrimp-fed and mussel-fed lobsters than the other groups.

DISCUSSION

5. DISCUSSION

5.1 Seasonal variation in the landing and proximate composition

The estimated 5.5 tonnes of spiny lobster landings contributed only 0.02% of the total landings at the Chennai Fisheries Harbour during February 1999 to January 2000 (Vivekanandan, personal communication). The Chennai Fisheries Harbour contributed 0.3% to the all India spiny lobster landings (2094 t in 1999; CMFRI, 2001). It is estimated that 74.3 % of the landings of the spiny lobsters at Chennai Fisheries Harbour was during the II half of the year (July - December). The landings in April and May 1999 were less due to closure of trawl fishery at Chennai during these months. Earlier studies indicated that the lobsters were most intensively caught between October and March along the southeast (Radhakrishnan, 1995) and southwest coasts (George, 1967) and between October and January along the northwest coast (Kagwade *et al.*, 1991) of India. The CMFRI (2001) observed that the peak spiny lobster catches by bottom set gill net at Kovalam near Chennai was during March and May. The CMFRI (1998) reported that the lobster landings in the III and IV quarters (II half of the year) contributed only 42.9 % to the annual landings along the Indian coast during 1997-98. These studies indicate the inconsistencies in the monthly spiny lobster landings along the Indian coast. Kagwade *et al.* (1991), Kagwade (1993), and Radhakrishnan and Manisseri (2001) also have reported the inconsistent seasonal abundance in the fishery of *P. homarus* and *P. polyphagus* along the Indian coast.

P. homarus contributed 77.6 % to the spiny lobster landings at Chennai. Earlier studies have also indicated *P. homarus* as the most dominant species along the Chennai coast (Kagwade *et al.*, 1991; CMFRI, 1997, 2000, 2001). *P. homarus* and *P. ornatus* dominate the spiny lobster landings all along the Indian coast, barring the northwest coast, where *P. polyphagus* dominate the fishery (George, 1973; Kagwade *et al.*, 1991; Kagwade, 1993; Vijayakumaran and Radhakrishnan, 1997).

The tail meat of *P. homarus* constituted 28.9 ± 0.3% of its total body weight; the energy content of the tail meat was 5065 kj/kg wet tail meat. Considering that these values for *P. homarus* represent the values for all the exploited species of spiny lobsters, it is estimated that the spiny lobster landings of 5532 kg at Chennai Fisheries Harbour yielded 1599 kg of tail meat, equivalent to 8.1×10^6 kj of energy in the twelve month study period. During 1996-97, the export price of lobsters ranged from Rs 374/kg (frozen lobster) to Rs 943/kg (live lobster) (MPEDA, 1998). In other words, the value of 1000 kj of lobster energy ranged from Rs 74 (frozen lobsters) to Rs 186 (live lobsters). The currency value of the lobster energy was considerably higher compared to that of the other exploited aquatic resources. The price of squid and sardines during the study period averaged to Rs 50/kg and Rs 30/kg, respectively (Devaraj and Vivekanandan, MS). The energy content of 1 kg of squids (present study) and sardines (Radhakrishnan, 1989) are 3520 kj and 4613 kj respectively. The estimated currency values for 1000 kj energy of squids (Rs 14) and sardines (Rs 7) were very low. Ironically, one unit energy of the lobsters and sardines may be nutritionally equal but the currency value of one unit energy of the live lobsters is about 27 times higher than that of the sardines.

The fortnightly fluctuations of almost all the body constituents, viz., water, protein, lipid, carbohydrate, ash and energy in the muscle, hepatopancreas and exoskeleton of the juveniles as well as maturing *P. homarus* were significantly different. However distinct trends in the fluctuations were not evident for any of the parameters. Fluctuations in the absence of distinct seasonal trends indicate individual-to-individual variations in the population. Similar individual variations, which mask the seasonal trend, were observed in several crustaceans (Table 27). Glycogen, carbohydrate, protein and non-protein nitrogen in the hepatopancreas and ovary of the crab *Carcinus maenas* (Heath and Barnes, 1970); water, protein, lipid, carbohydrate, ash and energy contents of the crab *Ovalipes punctatus* (Du Preez and Mc Lachlan, 1983); lipid and cholesterol content in the hepatopancreas,

Table 27. Seasonal variations in the biochemical composition of crustaceans

Sl. no.	Species	Study area	Temp. oC	Tissues	Estimated parameter	Trend in seasonal variation	Remarks	Reference
1	*Jasus lalandii*	Olifantbos and Hount Bay	N. A.	Abdominal Muscle	Water, protein, lipid, carbohydrate and ash	Absent	Nil	Cockcroft (1997)
2	Homarus americanus	Bonavista Bay	N. A.	Blood	Serum protein	Present	Seasonal variation due to moult cycle	Ennis (1973)
3	*Palinurus elephas*	N. A.	N. A.	Blood	Sub unit composition of haemocyanin	Present	Nil	Bellelli *et al.* (1988)
4	*Palinurus mauritanicus*	N. A.	N. A.	Blood	Sub unit composition of haemocyanin	Absent	Nil	Bellelli *et al.* (1988)
5	*Palinurus elephas*	N. A.	N. A.	Blood	Sub unit composition of haemocyanin	Present	Nil	Giardina *et. al.* (1986)
6	Indian lobster	India	N. A.	Hepato - pancreas	Fat	Present	Nil	George and Patel (1956)

7	*Penaeus semisulcatus*	Lebanonese Coast	N. A.	Whole body	Water, protein, lipid, carbohydrate and ash	Absent	Nil	Nuwayhid and Young (1985)
8	*Penaeus setiferus, P. aztecus* and *P.duorarum*	Corpus Christi Bay	27	Whole body	Fatty acids	Present	Seasonal variation due to changes in feed composition	Bottino *et al.* (1980)
9	*Pleoticus mulleri*	San Jorge Gulf	6.7-13.9	Ovary	Water, ash, lipidclass and fatty acids	Present	Seasonal variation due to changes in reproductive cycle	Jeckel et al. (1989a)
10	*Pleoticus mulleri*	San Jorge Gulf	6.7-13.9	Male reproductive system	Water, ash, lipidclass and fatty acids	Present	Seasonal variation due to changes in reproductive cycle	Jeckel et al. (1989b)
11	*Taphromysis bowmani*	Florida Estuary	20.3-27.6	Whole body	Protein, lipid, carbohydrate, chitin,ash and energy	Absent	Nil	Johnson and Hopkins (1978)

12	*Ovalepis punctatus*	Kings Beach and Maitlands River Beach	N. A	Whole body	Water, protein, lipid, ash, carbohydrate and energy	Absent	Nil	Du Preez and Mc Lachlan (1983)
13	*Carcinus maenas*	Milliport	N. A	Hepato-pancreas and ovary	Glycogen, neutral fat, carbohydrate, phospholipids	Absent	Changes due to changes during maturity	Heath and Barnes (1970)
14	*Neptunus pelagicus* and *Scylla serrata*	Sikka Coast	N. A	Hepato-pancreas, shoulder and claw muscle	Glycogen, lipid and cholestrol	Absent	Glycogen in hepato-pancreas shows variation with moult cycle	Senthikumar and Desai (1978)
15	*Scopimera globosa*	Waka Estuary	N. A	Whole body	Glycogen and lipid	Absent	Nil	Iwata et al. (1983)
16	*Callinectes sapidus*	N. A	N. A	Whole body	Amino acid	Present	Changes due to moult cycle	Thompson and Farragut (1966)

shoulder and claw muscle of the crabs *Neptunus pelagicus* and *Scylla serrata* (Senthikumar and Desai, 1978); water, protein, lipid, carbohydrate and ash content of the prawn *Penaeus semisulcatus* (Nuwayhid and Young, 1985); glycogen and lipid contents in the crab *Scopimera globosa* (Iwata *et al.*, 1983); protein, lipid, carbohydrate, chitin, ash and energy contents of the mysid shrimp *Taphromysis bowmani* (Johnson and Hopkins, 1978); water, protein, lipid, carbohydrate and ash contents in the abdominal muscle of the lobster *Jasus lalandii* (Cockcroft, 1997); and the subunit composition of heamocyanin of the lobster *Palinurus elephas* (Giardina *et al.*, 1986) are some examples for vast individual variations.

However, seasonal patterns in the biochemical variations were observed for a few crustaceans (Table 27). These patterns were related to (i) the moult cycle of the individuals in the population (Heath and Barnes, 1970; Ennis, 1973; Senthikumar and Desai, 1978; Du Preez and Mc Lachlan; Ferrer, 1988; and Cockcroft, 1997); or (ii) to the reproductive stages (George and Patel, 1956; Jeckel *et al.*, 1989 a, b, 1991); or (iii) due to changes in the biochemical composition of the food consumed (Bottino *et al.*, 1980).

Crustaceans in different stages of moult cycle are known to exhibit vast differences in their biochemical composition. During the moult cycle, pronounced biochemical changes have been observed between the intermoult, premoult and postmoult stages of the palinurid lobsters (Scheer and Scheer, 1951; Schwabe *et al.*, 1952; Travis, 1955a, b, 1957; Dall, 1977; Radhakrishnan, 1989). In the present study, however, only lobsters in the intermoult stage and in active growth phase were used for the analysis. Hence, moult cycle would not have interfered in the individual variations in the biochemical constituents.

The biochemical composition of the muscle, hepatopancreas, haemolymph and ovary of the crustaceans are reported to be influenced by the maturity stages (Khan and Natarajan, 1982; Asokan and George, 1984; Adiyodi, 1985; Castille and Lawrence, 1989;

Jeckel *et al.*, 1989a, b; Rahman, 1989; Teshima *et al.*, 1989; Huner *et al.*, 1990; Vijayakumaran, 1990; Tuck *et al.*, 1997; Cheng *et al.*, 2000; Palacios *et al.*, 2000; Wouters *et al.*, 2001; Sivachandrabose, 2002). In the present study, the term maturing lobster refers to the lobsters that were marginally larger (150-200 g weight) than the size at first maturity. *P. homarus* attains sexual maturity at about 50 mm carapace length and 140 g weight (Vijayakumaran, 1990). Considering the maximum size which *P. homarus* attains (weight = 1.5 kg) (Vijayakumaran, personal communication), the difference in the size between the two groups used in the present study is only marginal. Whereas the small size group lobsters were immature, the larger ones also were not reproductively active individuals. Hence, reproductive process would not have influenced the individual differences in the biochemical constituents.

In the present study, the presence of individual variations and the absence of a clear fortnightly pattern in the two size groups of *P. homarus* may be due to the following reasons:

i) The bivalves constitute the most preferred natural food of *P. homarus* (Berry, 1971; Smale, 1978). During the course of the present study, gut content analysis of lobsters collected from the landings were made, which revealed the presence of bivalve shells in several individuals of *P. homarus*. The bivalve resource is very rich throughout the year along the Chennai coast. The common bivalves are *Perna viridis*, *Paphia* spp., *Modiolus* spp., *Solen kempi*, *S. linearis*, *Laternula anatina*, *Tellina methoria* etc. (Thangavelu and Sanjeevaraj, 1988). Hence, the lobsters are exposed to consistent food supply in the form of different species of bivalves off Chennai. The proximate composition of these bivalves are different depending upon the type of the phytoplankton they consume (Giese, 1966). It is possible that the individual differences in the biochemical composition of the lobsters might be due to the differences in the biochemical composition of the phytoplankton transmitted to the individual lobsters through their food, the bivalves.

ii) Bivalves in different stages of gonadal maturity occur simultaneously in the population (Mane and Nagabhushanam, 1988; Victor and Subramoniam, 1988). The biochemical composition of the body tissues of the bivalves is directly related to their maturity cycle (Ansell, 1974 a, b, c; John, 1980; Balasubramanyan and Natarajan, 1988; Easterson and Kandasami, 1988). Consequently, the proximate composition of a lobster feeding on a juvenile bivalve may be different from the one feeding on a bivalve in ripe stage of gonadal maturity. It appears that the individual differences in the proximate composition of the lobster population may be related to the biochemical composition and physiological condition of the food organism consumed by the lobsters.

The annual average water, nutrient and energy contents greatly differed between the tissues (tail muscle, hepatopancreas and exoskeleton) of the lobster. Among the tissues, the water content was maximum (75.9%) in the tail muscle. The low water content in the hepatopancreas (63.7%) was due to its high lipid content whereas, in the exoskeleton (37.7%) it was due to the high ash content. The tail muscle exhibited the highest protein content (81.1%). The hepatopancreas of decapod crustaceans has long been recognized as the major site for storage of reserve lipid (Travis, 1955a, 1957; Allen, 1971; Gibson and Barker, 1979; Al-Mohanna and Nott, 1989). Due to the high lipid content, the energy content too was highest (24.6 kj/g dry weight) in the hepatopancreas. Ash formed the major component (93.8 % of dry weight) of the exoskeleton. The ash content in the exoskeleton of *P. homarus* is comparable with the values of other crustaceans. Du Preez and Mc Lachlan (1983) observed 92.1 % of dry weight as ash in the exoskeleton of the crab *Ovalipes punctatus* and the corresponding value for the American lobster *Homarus americanus* was 94.1% (Floreto *et al.*, 2000b). The nutrient components and energy content are very low in the exoskeleton.

5.2 Effect of starvation

Under starvation, the non-ablated *P.homarus* survived for 97 days. Crustaceans are known to survive for several weeks under complete starvation. The adult shore crab *Carcinus maenas* can survive upto 3 months of starvation with only 50% mortality (Wallace, 1973). Chittleborough (1975) observed that *Panulirus longipes* survived for 24 to 43 weeks under starvation. The subterranean aquatic crustaceans like *Niphargus rhenorhodanensis* and *N. virei* can survive without feeding for periods well in excess of one year (Mathieu and Gilbert, 1980). *Euphausia superba* can extremly tolerate starvation and are able to survive upto 7 months without food (Ikeda and Dixon, 1982). *Birgus latro* (the largest land dwelling crustacean) can survive periods more than a year without food (Storch *et al.* 1982). Hervant *et al.* (1997) pointed out that hypogean amphipod and isopod are better adapted to lack of food with survival period exceeding 200 days.

Several crustaceans are known to moult under starvation. It has been reported that the non-ablated prawns, *Palaemon lamarrei* (Katre and Reddy, 1976), *Macrobrachium lanchesteri* (Ponnuchami *et al.*, 1981) and *Metapenaeus monoceros* (Sumitra Vijayaraghavan *et al.*, 1982) moulted but with low frequency. These studies suggest moulting in the crustaceans as a metabolic necessity, occurring at the expense of stored organic reserves irrespective of food availability. In the present study, the non-ablated lobsters did not moult. However, they might have moulted, if they had been forced to starve from the premoult (D) stage, but the lobsters failed to moult since the starvation commenced in the intermoult (C) stage. The ablated *P. homarus* survived for only 48 days, i.e., only half the survival capacity of the non-ablated lobsters. Radhakrishnan (1989) observed survival duration of 69 and 53 days for the non-ablated and ablated *P. homarus* respectively under starvation. The ablated lobsters could not survive longer since they were forced to expend considerable energy towards moulting even under the stress of starvation. On the other hand, three ablated lobsters moulted once on the 46th, 51st and 52nd day of starvation but died 2 or 3 days after

moulting. The remaining *P. homarus* (n = 5), which did not moult, were in preparatory stages of moulting. This was evident from the formation of a second layer of integument beneath the outer layer. However, these lobsters also succumbed to death, as they could not progress further with the process of moulting. The removal of the eyestalk and thereby the Moult Inhibiting Hormone (MIH) has forced the ablated lobsters to moult or initiate the process related to moulting even under the stress of extreme starvation. The moult cycle is believed to be regulated by the interaction of two hormonal factors; the MIH, from the eyestalk neurosecretory complex, called the X-organ (Bliss, 1951; Passano, 1951; Aiken and Waddy, 1992) and the moulting hormone, from a non-neural endocrine gland called Y-organ (Gabe, 1953, 1954). The relationship between eyestalk removal (removal of MIH) and the accelerated moulting in decapods was established by Passano (1953), Quackenbush and Herrnkind (1981), Radhakrishnan and Vijayakumaran (1982, 1984, 1987), Radhakrishnan (1989) and Zhang *et al.* (1997). Under starvation, the ablated lobster probably would have utilized the stored energy from the hepatopancreas towards moulting. The energy expenditure towards the elevated metabolism due to the moulting process and the energy lost as moult would have resulted in shorter survival period of the ablated lobsters.

Hence, it may be concluded that occurrence of moulting is dependent on the nutritional and physiological status of the non-ablated lobster, whereas the ablated lobster could not avoid moulting; whatever may be their nutritional status.

The ablated lobster (weight loss: 730 mg/d) lost live body weight at about 80% higher rate than the non-ablated lobster (weight loss: 410 mg/d) during starvation. The loss in the rate of live body weight was three times (1300 mg/d) higher than that for the non-ablated lobster if the moult is also considered. The rate of weight loss was very high during the first 6 weeks of starvation in both the ablated and non-ablated lobsters. In the subsequent weeks, the lobsters managed to survive with marginal weight loss. Studies on the physiological processes underlying

growth have suggested that the basic maintenance metabolic requirement of an animal must be satisfied by the energy intake before the energy is made available for other body functions (Paloheimo and Dickie, 1966). The restriction of loss of body weight after 6 weeks of starvation may be due to the non-availability of energy for any other body functions except for the basal metabolism. The ablated lobsters, however, were under the additional stress, *viz.* moulting, and hence lost weight through moult during the 6-8 weeks of starvation.

The condition of hepatopancreas is intimately associated with numerous environmental parameters, and it can be used to evaluate the nutritional status of animals (Papathanassiou and King, 1984; Vogt *et al.*, 1985, 1986, 1989; Whyte *et al.*, 1986). Under starvation, the lipid content in the hepatopancreas of the non-ablated and ablated lobsters drastically declined from 33.6% to 17.6%, and to 14.0%, respectively. For survival, the ablated lobsters utilized lipid at a higher rate compared to that of the non-ablated lobster. The energy content of the ablated lobsters decreased from 25.7 kj/g (control at the beginning of the experiment) to 18.4 kj/g at the time of death i.e., a reduction at the rate of 132.7 j/g/d compared to the loss of only 72.3 j/g/d by the non-ablated lobster. The energy content in the muscle reduced from 21.2 kj/g at the start of the experiment to 19.4 kj/g in the non-ablated and 17.7 kj/g in the ablated lobsters, i.e., the rate of energy loss was 16.8 j/g/d and 30.9 j/g/d, respectively. The reduction of energy content in the exoskeleton was more (62.5% of the initial value) when compared to that of the hepatopancreas (21.0% and 28.4% in the non-ablated and ablated lobsters, respectively) and muscle (8.5% and 16.5% in the non-ablated and ablated lobsters, respectively). At the time of death, the energy content in the exoskeleton of the non-ablated and ablated lobsters was only about 35% of that of the control lobsters. In the exoskeleton, the energy content reduced from 0.08 kj/g to 0.03 kj/g in both the non-ablated and ablated lobsters. The corresponding rate of loss of energy was 0.50 j/g/d in the non-ablated and 0.91 j/g/d in the ablated lobsters. Under starvation, the lobsters regulated the allocation of lipid and energy

for the maintenance of exoskeleton at a very low level compared to the allocation for the muscle and hepatopancreas. Lipid serves as an important endogenous energy reserve in marine invertebrates, and a reduction in total lipids in response to starvation has been reported for the adults and sub-adults of *Penaeus duorarum*, *P. japonicus* and *P. esculentus* (Schafer, 1968; Cuzon *et al.*, 1980; Barclay *et al.*, 1983). The advantage of lipid versus carbohydrate as a metabolic fuel is well documented (Hochachka and Somero, 1973). Vogt *et al.* (1985) noted a reduction in the lipid droplets in the hepatopancreas of the postlarvae of *P. monodon* between the first and third day of starvation.

Consistent with earlier studies (Stewart *et al.*, 1967, 1972 for *H. americanus*; Schafer, 1968 for *Penaeus duorarum*; Cuzon *et al.*, 1980 for *P. japonicus*; Whyte *et al.*, 1986 for *Pandalus platyceros*; Evans *et al.*, 1992 for *Cherax tenuimanus*; Jones and Obst, 2000 for *Cherax destructor*), it has been demonstrated in the present study, that reduction in size and nutrient content of the hepatopancreas occurs when crustaceans are starved. The hepatosomatic index of *P. homarus* reduced from 4.70% to 1.75% in the non-ablated lobsters and to 1.64% in the ablated lobsters. It appears that hepatosomatic index of about 1.7% is essential for performing the minimal metabolic activities of the lobsters. The reduction in the hepatosomatic index upon starvation is 62.8% and 65.1% in the normal and ablated lobsters, respectively. In the present study, a strong relatioship between the duration of starvation and HSI_d has been obtained for the control ($r = 0.9490$) and ablated ($r = 0.9878$) *P. homarus*, suggesting that the HSI_d between 4.7 and 1.7% may indicate a continuum between an active feeding status and death due to total food nonavailability.

Unlike the lipid and energy contents, the water and ash contents increased in the muscle, hepatopancreas and exoskeleton of the ablated as well as the non-ablated lobsters. A similar increase in water content has been reported for *Panulirus longipes* (Dall, 1974); *Penaeus japonicus* (Cuzon *et al.*, 1980); *Penaeus esculentus* (Barclay *et al.*, 1983); *H. americanus* (Sasaki, 1984); *P. homarus* (Radhakrishnan,

1989); *Penaeus vannamei* (Stuck *et al.*, 1996); and *Niphargus vieri*, *N. rhenorhodanensis*, and *Gammarus fossarum* (Hervant *et al.*, 1999). Gu *et al.* (1996) have demonstrated that starvation increased the whole body water content in the juvenile red claw crayfish, *Cherax quadricarinatus*. During starvation, energy is derived solely from endogenous resources, and tissues are lost due to catabolic activities. To maintain the necessary body volume and internal turgidity during starvation, the lost tissue mass must be replaced by water (Heath and Barnes, 1970; Dall, 1974; Wilcox and Jeffries, 1976). The ash content increased, as the organic content decreased, probably due to an increase in alkaline metals (Mayzaud, 1976). Surprisingly, the protein content in the hepatopancreas (in terms of dry weight) increased from 55.2% in the control lobsters to 65.2% in both the non-ablated and ablated lobsters at the time of death. It appears that the lobsters have the capacity to convert the stored lipid/carbohydrate into proteins under conditions of extreme starvation. Perhaps storage of protein is advantageous for performing the basal metabolic activities and for prolonging the survival of the lobsters.

5.3 Effect of different food on food utilization

Depending upon the type of food, *P. homarus* consumed 209.6 (squid) to 263.5 (mussel) j/g/d i.e., the lobster has the capacity to increase the feeding rate by 25.7% under *ad libitum* feeding regime. Radhakrishnan (1989) reported 52.7% higher feeding rate in *P. homarus* exposed to mixed food (combination of *Perna viridis*, *Meretrix casta* and a clupeid fish; 371.3 j/g/d) compared to the group exposed to the mussel *P. viridis* (243.2 j/g/d). Clearly, the feeding rate of *P. homarus* is influenced by the type of food offered.

Several predatory crustaceans like the crab *Scylla serrata* (Hill, 1976), *Carcinus maenas* (Walne and Dean, 1972; Elner and Hughes, 1978), *Portunus puber* (Ebling *et al.*, 1964), *Ovalipes punctatus* (Du Preez, 1984) and the American lobster, *H. americanus* (Ennis, 1973; Elner and Jamieson, 1979) prey mainly upon hard-shelled molluscs. The palinurid lobsters like *P. homarus* (Berry, 1971; Smale, 1978), *P. cygnus*

(Joll and Phillips, 1984), *P. interruptus* (Shaw, 1986) and *Jasus lalandii* (Newman and Pollock, 1974; Pollock, 1979, 1982; Griffiths and Seiderer, 1980) also prey predominantly on molluscs, especially the bivalves. In the present study, the lobster consumed the mussels at the highest feeding rate (263.5 j/g/d) but the rate of consumption by the clam-fed group was comparatively low (235.6 j/g/d).

Irrespective of the type of food consumed, *P. homarus* exhibited uniformly high assimilation efficiency (96.7% to 98.2%). The assimilation efficiency determined in the present study may be marginally an overestimate. The faecal matter was collected from the experimental aquaria at intervals of 24 hours. The agitation of water caused by the aerator and by the experimental animals would have dissolved some of the faecal matter. Moreover, nitrogen excretion was estimated as the amount of ammonia excreted. The pattern of nitrogen excretion in *P. homarus* is typical of that of several aquatic invertebrates (Prosser and Brown Jr., 1961), in which the principal excretory product of the animal is ammonia. Parry (1960) and Pandian (1975) reported that urea, aminoacids, purines and uric acid are the other nitrogenous excretory products of marine crustaceans in addition to ammonia. Though the contribution of these nitrogenous excretory products to the total nitrogen excretion is negligible, the estimation of only ammonia, and the dissolved faeces would have resulted in marginal overestimation of assimilation. Nevertheless, high assimilation rates are not uncommon in the crustaceans. In *P. homarus*, the assimilation efficiency was 97.1 - 98.8 % (Radhakrishnan, 1989) and 93.7 - 97.1 % (Vijayakumaran, 1990). Efficiency of assimilation was 97.8% for the grass shrimp *Palaemonetes pugio* (Vernberg and Piyatiratitivorakul, 1998); 82% for *H. americanus* (Logan and Epifanio, 1978) and above 90 % for the giant fairy shrimp *Branchinecta gigas* (Daborn, 1975). The assimilation efficiency of the prawns *Palaemon serratus*, *Pandalus platyceros* (Forster and Gabbot, 1971), *Penaeus setiferus*, *P. aztecus* (Condrey *et al.*, 1972) and *Metapenaeus bennettae* (Moriarty, 1977) ranged from 97.0 to 98.0 %.

Marian *et al.* (1986) observed assimilation efficiency of 94% (tubifex-fed) and 88% (goat liver-fed) for the prawn *Macrobrachium lamarrei.*

The type of consumed food has considerably influenced the conversion rate. The conversion rate ranged between 14.6 j/g/d (squid-fed) and 23.9 j/g/d (clam-fed). In other words, the conversion rate was about 60 % higher in the clam-fed group than in the squid-fed group. Irrespective of lower feeding rate, the conversion rate of the clam-fed group was 15% higher than that of the mussel-fed group, which had the highest consumption rate. The difference in the conversion rate may be due to the difference in the biochemical composition of the feed. In spite of the low feeding rate, the clam-fed group exhibited the maximum rate and efficiency of conversion (K_2: 10.4 %), suggesting that the group feeding at maximum rate did not convert the consumed food at maximum efficiency, an observation recorded for many fishes (Pandian, 1967; Gerking, 1971; Vivekanandan, 1976). The higher conversion rate by the clam-fed group is reflected by a short intermoult duration. The intermoult duration in the clam-fed group was only 42.7 days compared to 52.3 days in the squid-fed group. Live weight increase ranged between 323.2 mg/d (squid-fed) and 628.3 mg/d (clam-fed). The increase in live weight was comparable with the earlier studies on *P. homarus* (Srikrishnadhas *et al.*, 1983: 605.4 mg/d in marine cages; Radhakrishnan and Vijayakumaran, 1984: 350.0 mg/d with mussel/clam feeding initially followed by fish; Radhakrishnan, 1989: 207.9 (mussel, clam-fed) to 326.7 mg/d (mixed food); Vijayakumaran, 1990: 353.7 mg/d with clam feed; CMFRI, 2000: 652.1 mg/d with mussel, clam and trash fish as feed). However, higher growth rates were observed for *P. homarus* (Rahman *et al.*, 1994: 1151.2 mg/d) and *P. polyphagus* in the inter-tidal pit culture along Bhavnagar coast using trash fish and natural fauna as food (Sarvaiya, 1987: 1250.0 to 1388.9 mg/d; Philipose, 1994: 833.3 to 1000.0 mg/d). The reasons for the high growth rates reported in the pit culture were due to the regular water exchange in the ponds through tidal inflow and high productivity in the culture pits. On the other hand, low growth rates were observed for *Jasus edwardsii* (Rayns, 1991: 39 mg/d

fed with *Austrovenus stutctburyi*; Hooker *et al.*, 1997: 85 mg/d, 160 mg/d and 180 mg/d respectively in 0+, 1+ and 2+ year classes fed with green lip mussel, *Perna canaliculatus*). The slow growth rate may be due to the low temperature (8 to 18^0 C) to which those species were exposed. The growth rate of different species of lobsters varies enormously (39.0 to 1388.9 mg/d) as a result of factors such as temperature and other environmental conditions, habitat and rearing conditions (Fielder, 1964; and Kittaka and Booth, 1994).

P. homarus converted 3.2 to 3.9% (3.5 $\pm$ 0.3%) of the consumed energy for production of moult. The shrimps *Penaeus stylirostris* and *P. vannamei* utilized less than 3% of the consumed energy for moult production (Cousin, 1995). The energy lost through moult ranged from 26.4% (clam-fed) to 36.0% (squid-fed) and averaged to 29.8 $\pm$ 4.3% of the converted energy. The loss through moult is comparable to those reported for several crustaceans. Radhakrishnan (1989) and Vijayakumaran (1990) observed that 27.3% to 32.7% of the converted energy was used for moult production by *P. homarus*. The crab *Menippe mercenaria* lost 22.7% of the converted energy as moult (Mootz and Epifanio, 1974). The freshwater prawn, *Macrobrachium lanchesteri* lost as high as 58.9% of the converted dry matter as moult (Ponnuchamy *et al.*, 1981).

Food utilization parameters are influenced by the biochemical constituents of the consumed food. It appears that *P. homarus* requires a right combination of biochemical constituents in the food for achieving maximum rate and efficiency of conversion. Among the experimental food, *P. indicus* had the highest protein content (68.6%) and a high lipid content (8.8%) but the lowest carbohydrate content (4.4%). This combination could not induce higher rate (21.3 j/g/d) and efficiency (8.9%) of conversion for the lobster. The clam *Paphia malabarica* had the lowest protein content (56.8%) but the highest carbohydrate content (24.4%). In spite of the low protein and lipid contents, the energy content (17.9 kj/g) was high in the clam. The high energy content in the clam was essentially through carbohydrate unlike

the other food items such as mussel, shrimp and squid. Brown *et al.* (1989) observed that high carbohydrate content in the feed failed to show high feeding rate in the crayfish *Procambarus clarkii*. However, high levels of carbohydrate were found to be important for achieving maximum conversion rate of *P. clarkii* (Brown *et al.*, 1986).

The metabolic rate of *P. homarus* was directly proportional to the feeding rate. On an average, the metabolic rate contributed 85.7 % to the consumed energy. As *P. homarus* is gregarious in behaviour, isolated rearing might have induced higher metabolic rate. However, in the wild lobsters, the metabolic rate may be higher, since the animal has to spend considerable energy on locomotion for food securing. Moreover, the different food items offered to the lobsters were in an almost ready-to-eat form *i.e.*, the shrimp was offered as small pieces after removing the head; the squid after removing the intestine and suckers; and the clam and mussel after removing the shell. Hence, compared to the wild lobsters, the lobsters in the present experiment would have spent less energy towards the processes related to seizing and extracting the food. In the wild, the lobsters have to crush the bivalve shells with mandibles, insert the dactylus of the first two pairs of walking legs between the shells, prise the shells apart and scoop the meat. Barkai and Branch (1988) found that 81% of the total daily energy requirement of *Jasus lalandii* was used for respiration under natural conditions. Marian *et al.* (1986) estimated that 80.2%, 86.5% and 79.5% of the consumed energy were spent for metabolism by *Macrobrachium lamarrei* fed with *Tubifex tubifex*, goat liver and carrot, respectively.

The mean rate of oxygen consumption (0.43 ml O_2/g/h) calculated in the present study is higher than that reported for several temperate crustaceans. The oxygen consumption of the tropical crustaceans, which are exposed to water temperatures of 24 to 29°C range from 0.12 to 0.65 ml O_2/g/h (Table 28). In comparison, the oxygen consumption of the temperate crustaceans, which are exposed to water temperatures of 15 to 22°C, range from 0.02 to 0.10 ml O_2/g/h. Thus, there is 30 times difference between the highest and lowest rates of

Table 28 Oxygen consumption of lobsters and crayfishes in different temperature regimes

Sl. no.	Species	Water temperature (^{0}C)	O_2 consumption (ml O_2/g/h)	Reference
1	*Homarus americanus*	5	0.030	Mc Leese and Watson, 1968
2	*Jasus lalandii*	8-19	0.019-0.051	Zoutendyk, 1989
3	*Homarus americanus*	9-10	0.020	Penkoff and Thurberg, 1982
4	*Homarus americanus*	12-25	0.044-0.088	Mc Leese, 1964
5	*Panulirus interruptus*	13-20	0.034-0.066	Winget, 1969
6	*Homarus gammarus*	15	0.068	Jolyet and Regnard, 1877
7	*Palinurus elephas*	15	0.044	Jolyet and Regnard, 1877
8	*Homarus americanus*	15	0.020	Bosworth *et al.*, 1936
9	*Astacus astacus*	15	0.030-0.054	von Buddenbrock, 1948
10	*Homarus vulgaris*	15	0.040-0.077	Thomas, 1954
11	*Homarus vulgaris*	15	0.027	Butler *et al.*, 1978
12	*Austropotamobius leptodactylus*	19-21	0.070	Bishop, 1950
13	*Austropotamobius torrentium*	19-21	0.100	Bishop, 1950
14	*Homarus americanus*	22	0.037-0.039	Bosworth *et al.*, 1936
15	*Panulirus homarus*	24-25	0.53	Radhakrishnan, 1989
16	*Panulirus homarus*	24-27	0.43	Present study
17	*Procambarus alleni*	25	0.066	Davison, 1956
18	*Panulirus homarus*	25-28	0.27	Vijayakumaran, 1990
19	*Panulirus argus*	27	0.121	Buesa, 1979
20	*Panulirus guttatus*	27	0.147	Buesa, 1979
21	*Cambarellus shufeldtii*	29	0.34-0.65	Fingerman, 1955

oxygen consumption in the crustaceans listed in Table 28.

At the end of the experiment, the water, protein and lipid contents in the muscle, hepatopancreas and exoskeleton of *P. homarus* were significantly different from the corresponding values at the beginning of the experiment. Whereas the water and protein contents decreased in the three tissues of the lobster receiving four different types of food, the lipid content increased at the end of the experiment. In the muscle, for instance, the lipid contributed 19.4 % and 21.0 % at the beginning and at the end of the experiment, respectively; the corresponding values for hepatopancreas were 51.3 % and 54.2 %. However, compared to the water, protein and lipid contents, the energy content of the lobster at the commencement and at the end of the experiment did not differ appreciably. It appears that, under controlled conditions, the lobster has the tendency to store the energy in the form of lipid rather than as protein. Combustion of lipids, compared to protein and carbohydrates, requires higher oxygen (2.0×10^3, 1.2×10^3 and 0.8×10^3 ml O_2/g for lipid, protein and carbohydrate, respectively; Crisp, 1976). On the other hand, combustion of lipids provides nearly twice as much energy per unit weight (Gnaiger, 1983), and hence lipids are more efficient for energy storage (Crisp, 1976). Prior to the commencement of the experiment, the lobsters collected from the wild were reared for 10 days in the laboratory and the control lobsters were sacrificed on the 10^{th} day. The experiment lasted for 105 days. Hence, the lobsters would have retained the characteristics of the wild population at the commencement of the experiment compared to those at the end of the experiment. In the 115 days of laboratory rearing, in which the availability of food was not a constraint, the lobsters shifted their mode of storage from protein-based energy to lipid-based energy.

The Food Conversion Ratio (FCR) for growth (P) ranged between 2.7 and 4.1. The FCR was comparable with that of the earlier studies on spiny lobsters (4.1 in the clam-fed *P. homarus*, Vijayakumaran and Radhakrishnan, 1984; 4.7 in the mussel-fed *P. ornatus*, Radhakrishnan and Vijayakumaran, 1987; 2.4 - 8.3 in *P. homarus* fed

with mussel, clam, fish and mixed feed, Radhakrishnan, 1989; and 1.79 - 5.12 in the clam-fed *P. homarus*, Vijayakumaran, 1990). However, the FCR values for the spiny lobsters are considerably lower than those reported for other decapods such as *H. americanus* fed on pellet feed (45.1; Castell *et al.*, 1977), *Cherax destructor* (5 to 12; Mills and Mc Cloud, 1983). Meanwhile, Crear *et al.* (2000) recorded a FCR of 1.26 (mussel-fed), 2.24 (prawn-fed) and 3.78 (pellet-fed) in the juvenile *Jasus edwardsii* grown at ambient temperature.

SUMMARY

SUMMARY

1. The estimated spiny lobster landings at Chennai Fisheries Harbour were 5532 kg during February 1999 and January 2000. Good landings were observed between July and January.

2. The landings comprised of *Panulirus homarus* (77.6%), *P. polyphagus* (15.2%), *P. ornatus* (5.0%), and *P. versicolor* (2.2%).

3. The high-value tail muscle constituted 28.9 $\pm$ 0.3% of the total wet weight of *P. homarus*. The tail muscle realised from the landings of *P. homarus* was 1241.1 kg, and 1599.2 kg from the total spiny lobster landings during the 12 month study period.

4. The tail muscle of *P. homarus* yielded 242.3 kg, 32.3 kg and 5.0 kg of protein, lipid and carbohydrate, respectively, equivalent to 6.3 x 10^6 kj energy; and if all the 4 species yielded 312.3 kg, 41.4 kg and 6.4 kg of protein, lipid and carbohydrate, respectively, equivalent to 8.1 x 10^6 kj energy during the 12 months.

5. To determine the possible seasonal variations in the proximate composition, samples were collected every fortnight and the water, protein, lipid, carbohydrate, ash and energy contents were analysed in the tail muscle, hepatopancreas and exoskeleton of juveniles (50-100 g size) and maturing (150-200 g size) *P. homarus*. In the tail muscle of *P. homarus*, the water, protein, lipid, carbohydrate, ash and energy contents were 75.9 $\pm$ 2.0%, 81.1 $\pm$ 0.8%, 9.8 $\pm$ 1.0%, 1.7 $\pm$ 0.3%, 7.4 $\pm$ 1.0% and 21.0 $\pm$ 0.5 kj/g respectively during the 12 month study period.

6. In the hepatopancreas, the water, protein, lipid, carbohydrate, ash and energy contents were 63.7 $\pm$ 1.8%, 56.3 $\pm$ 1.2%, 31.6 $\pm$ 1.8%, 5.6 $\pm$ 0.7%, 6.5 $\pm$ 0.9% and 24.6 $\pm$ 0.7 kj/g, respectively.

7. In the exoskeleton, the water, protein, lipid, carbohydrate, ash and energy contents were 37.7 ± 1.7%, 3.5 ± 0.3%, 1.0 ± 0.2%, 1.7 ± 0.2%, 93.8 ± 0.4% and 0.09 ± 0.01 kj/g, respectively.

8. Laboratory experiments were conducted to assess the effect of starvation on the survival, hepatosomatic index, weight loss and changes in the proximate composition and energy contents in the tail muscle, hepatopancreas and exoskeleton of the normal and bilaterally eyestalk ablated *P. homarus*. The starved control *P. homarus* survived for 97.0 ± 5.3 days but the ablated lobster for only 48.3 ± 4.8 days. The control lobsters did not moult; 3 ablated lobsters moulted once during the period of starvation.

9. The control starved *P. homarus* lost 37.1% of the initial wet weight, whereas, the ablated lost 51.6% (which includes the weight lost through moult).

10. The dry hepatosomatic index (HSI_d) decreased from 4.72% to 1.75% in the control and to 1.64% in the ablated *P. homarus*.

11. In the tail muscle of the control and ablated *P. homarus*, the water, protein, lipid, carbohydrate, ash and energy contents changed from 72.9 to 79.4% and 85.5%; from 80.5 to 84.1% and 78.4%; from 10.2 to 5.1% and 6.1%; from1.9 to 1.1% and 1.7%; from 7.4 to 9.7% and 13.8%; and from 21.2 to 19.4 kj/g and 17.7 kj/g, respectively under starvation.

12. In the hepatopancreas of the control and ablated *P. homarus*, the water, protein, lipid, carbohydrate, ash and energy contents changed from 64.2 to 84.3% and 87.6%; from 55.2 to 65.2% and 65.2%; from 33.6 to 17.6% and 14.0%; from 6.0 to 5.3% and 5.7%; from 5.2 to 11.9% and 15.1%; and from 25.7 to 20.3 kj/g and 18.4 kj/g, respectively under starvation.

13. In the exoskeleton of the control and ablated *P. homarus*, the water, protein, lipid, carbohydrate, ash and energy contents changed

from 36.4 to 37.7% and 37.8%; from 3.6 to 2.8% and 2.7%; from 0.9 to 0.4% and 0.3%; from 1.5 to 1.0% and 1.0%; from 94.0 to 95.9% and 96.1%; and from 0.08 to 0.03 kj/g and 0.03 kj/g, respectively under starvation.

14. The protein-energy ratio of the control and ablated *P. homarus* in the tail muscle, hepatopancreas and exoskeleton increased from 0.159 to 0.182 and 0.185; from 0.0898 to 0.1343 and 0.1479; and from 1.95 to 2.55 and 5.51 respectively under starvation.

15. The effect of different food items *viz.*, shrimp, squid, clam and mussel on the food utilization of *P. homarus* was studied. The protein content was highest in the shrimp (68.6 ± 0.9%) and lowest in the clam (56.8 ± 1.3%). The lipid content ranged from 5.0 ± 0.7% (squid) to 10.2 ± 1.1% (mussel). The clam had the highest carbohydrate content (24.4 ± 1.4%) and the shrimp the lowest (4.4 ± 0.8%). Ash content varied between 18.1 ± 0.8% (shrimp) and 11.2 ± 0.6% (clam). Mussel had the highest energy content (18.3 ± 0.7 kj/g) and the shrimp the lowest (16.2 ± 0.4 kj/g).

16. The maximum feeding rate (263.45 ± 20.29 j/g/d) was observed in the mussel-fed *P. homarus* and the minimum (209.62 ± 20.68 j/g/d) in the squid-fed group.

17. Assimilation efficiency was very high in all the groups ranging from 96.7% to 98.2%.

18. Conversion rate excluding moult was highest in the clam-fed lobsters (23.9 ± 1.0 j/g/d) and lowest in the squid-fed lobsters (14.6 ± 1.5 j/g/d). The gross (K_1) and net (K_2) conversion efficiencies were10.2 ± 0.7% and 10.4 ± 0.7% for the clam-fed and 6.9 ± 0.1% and 7.1 ± 0.1% for the squid-fed lobsters. The conversion rate including moult was highest in the clam-fed lobsters (32.4 ± 0.9 j/g/d) and the lowest in the lobsters fed with squid (22.7 ± 1.2 j/g/d). The gross (K_1) and net (K_2) conversion efficiencies including moult were13.8 ± 0.8% and 14.1 ±

0.8% for the clam-fed and 10.9 ± 0.5% and 11.1 ± 0.5% for the squid-fed lobsters, respectively.

19. The metabolic rate was highest in the group receiving mussels (227.6 ± 19.5 j/g/d or 0.47 ± 0.04 ml O_2/g/h) and lowest in the squid-fed group (183.2 ± 19.5 j/g/d or 0.38 ± 0.04 ml O_2/g/h).

20. The intermoult duration was longest in the squid-fed lobsters (52.3 ± 2.5 days) and shortest (42.7 ± 1.5 days) in the clam-fed lobsters. Live weight gain excluding moult was maximum in the clam-fed lobsters (66.0 ± 3.2 g) and very low in the squid-fed lobsters (33.9 ± 0.9 g). The corresponding values including moult were 135.6 ± 3.8 g and 91.0 ± 10.3 g.

21. The estimation of energy budget for *P. homarus* revealed that 84.1 to 87.4% of the consumed energy was spent on metabolism, and 1.8 to 3.3% on excretion. Energy used for growth was 10.9 to 13.8% including moult and 6.9 to 10.2% excluding moult. It is estimated that 3.3 to 3.9% of the consumed energy was used for production of moult.

22. Food Conversion Ratio (FCR) ranged between 2.74 ± 0.17 (clam-fed lobsters) and 4.08 ± 0.06 (squid-fed lobsters) excluding moult and the corresponding values including moult were 1.33 ± 0.06 and 1.53 ± 0.13.

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APPENDICES

APPENDICES

Appendix 1. Summary of ANOVA for the proportion of dry weight of the tail muscle (1a) and hepatopancreas (1b) to the total dry mass of juvenile (body size: 50-100g) and maturing (body size: 150-200g) *P. homarus*

Appendix 1a

Source of variation	df	MS	F	P
Fortnight	23	0.186	0.793	> 0.05
Residual	360	0.234		
Total	383			

Appendix 1b

Source of variation	df	MS	F	P
Fortnight	23	0.037	1.287	> 0.05
Residual	360	0.029		
Total	383			

Appendix 2. Summary of ANOVA for the water content in the tail muscle (2a), hepatopancreas (2b) and exoskeleton (2c) of juvenile (body size: 50-100g) and maturing (body size: 150-200g) *P. homarus*

Appendix 2a

Source of variation	df	MS	F	P
Fortnight	23	0.007	0.992	> 0.05
Residual	360	0.007		
Total	383			

Appendix 2b

Source of variation	df	MS	F	P
Fortnight	23	3.593	4.290	< 0.01
Residual	360	0.838		
Total	383			

Appendix 2c

Source of variation	df	MS	F	P
Fortnight	23	2.668	2.249	< 0.01
Residual	360	1.188		
Total	383			

Appendix 3. Summary of ANOVA for the protein content in the tail muscle (3a), hepatopancreas (3b) and exoskeleton (3c) of juvenile (body size: 50-100g) and maturing (body size: 150-200g) *P. homarus*

Appendix 3a

Source of variation	df	MS	F	P
Fortnight	23	1.166	0.914	> 0.05
Residual	360	1.276		
Total	383			

Appendix 3b

Source of variation	df	MS	F	P
Fortnight	23	0.739	0.735	> 0.05
Residual	360	1.006		
Total	383			

Appendix 3c

Source of variation	df	MS	F	P
Fortnight	23	1.107	4.493	< 0.01
Residual	360	0.246		
Total	383			

Appendix 4. Summary of ANOVA for the lipid content in the tailmuscle (4a), hepatopancreas (4b) and exoskeleton (4c) of juvenile (body size: 50-100g) and maturing (body size: 150-200g) *P. homarus*

Appendix 4a

Source of variation	df	MS	F	P
Fortnight	23	3.670	5.391	< 0.01
Residual	360	0.681		
Total	383			

Appendix 4b

Source of variation	df	MS	F	P
Fortnight	23	12.605	1.634	< 0.05
Residual	360	7.716		
Total	383			

Appendix 4c

Source of variation	df	MS	F	P
Fortnight	23	0.525	2.147	< 0.01
Residual	360	0.244		
Total	383			

Appendix 5. Summary of ANOVA for the carbohydrate content in the tail muscle (5a), hepatopancreas (5b) and exoskeleton (5c) of juvenile (body size: 50-100g) and maturing (body size: 150-200g) *P. homarus*

Appendix 5a

Source of variation	df	MS	F	P
Fortnight	23	2.359	7.043	< 0.01
Residual	360	0.335		
Total	383			

Appendix 5b

Source of variation	df	MS	F	P
Fortnight	23	3.059	7.815	< 0.01
Residual	360	0.391		
Total	383			

Appendix 5c

Source of variation	df	MS	F	P
Fortnight	23	0.326	1.836	< 0.01
Residual	360	0.177		
Total	383			

Appendix 6. Summary of ANOVA for the ash content in the tail muscle (6a), hepatopancreas (6b) and exoskeleton (6c) of juvenile (body size: 50-100g) and maturing (body size: 150-200g) *P. homarus*

Appendix 6a

Source of variation	df	MS	F	P
Fortnight	23	2.499	2.767	< 0.01
Residual	360	0.903		
Total	383			

Appendix 6b

Source of variation	df	MS	F	P
Fortnight	23	3.365	3.309	< 0.01
Residual	360	1.017		
Total	383			

Appendix 6c

Source of variation	df	MS	F	P
Fortnight	23	0.982	0.285	> 0.05
Residual	360	3.443		
Total	383			

Appendix 7. Summary of ANOVA for the energy content in the tail muscle (7a), hepatopancreas (7b) and exoskeleton (7c) of juvenile (body size: 50-100g) and maturing (body size: 150-200g) *P. homarus*

Appendix 7a

Source of variation	df	MS	F	P
Fortnight	23	1.005	3.890	< 0.01
Residual	360	0.257		
Total	383			

Appendix 7b

Source of variation	df	MS	F	P
Fortnight	23	1.871	2.972	< 0.01
Residual	360	0.630		
Total	383			

Appendix 7c

Source of variation	df	MS	F	P
Fortnight	23	0.0007	0.992	> 0.05
Residual	360	0.0007		
Total	383			

Appendix 8. Summary of ANOVA for the water content in the tail muscle of the control (8a) and ablated (8b) *P. homarus* under starvation

Appendix 8a

Source of variation	df	MS	F	P
Weeks of starvation	8	7.218	43.896	< 0.01
Residual	27	0.164		
Total	35			

Appendix 8b

Source of variation	df	MS	F	P
Weeks of starvation	6	33.466	71.489	< 0.01
Residual	21	0.468		
Total	27			

Appendix 9. Summary of ANOVA for the protein content in the tail muscle of the control (9a) and ablated (9b) *P. homarus* under starvation

Appendix 9a

Source of variation	df	MS	F	P
Weeks of starvation	8	4.807	7.168	< 0.01
Residual	27	0.671		
Total	35			

Appendix 9b

Source of variation	df	MS	F	P
Weeks of starvation	6	2.255	3.741	< 0.05
Residual	21	0.603		
Total	27			

Appendix 10. Summary of ANOVA for the lipid content in the tail muscle of the control (10a) and ablated (10b) *P. homarus* under starvation

Appendix 10a

Source of variation	df	MS	F	P
Weeks of starvation	8	16.023	117.642	< 0.01
Residual	27	0.136		
Total	35			

Appendix 10b

Source of variation	df	MS	F	P
Weeks of starvation	6	9.453	68.144	< 0.01
Residual	21	0.139		
Total	27			

Appendix 11. Summary of ANOVA for the carbohydrate content in the tail muscle of the control (11a) and ablated (11b) *P. homarus* under starvation

Appendix 11a

Source of variation	df	MS	F	P
Weeks of starvation	8	2.255	53.609	< 0.01
Residual	27	0.042		
Total	35			

Appendix 11b

Source of variation	df	MS	F	P
Weeks of starvation	6	0.198	4.432	< 0.01
Residual	21	0.045		
Total	27			

Appendix 12. Summary of ANOVA for the ash content in the tail muscle of the control (11a) and ablated (11b) *P. homarus* under starvation

Appendix 12a

Source of variation	df	MS	F	P
Weeks of starvation	8	2.219	15.383	< 0.01
Residual	27	0.144		
Total	35			

Appendix 12b

Source of variation	df	MS	F	P
Weeks of starvation	6	14.444	86.469	< 0.01
Residual	21	0.167		
Total	27			

Appendix 13. Summary of ANOVA for the energy content in the tail muscle of the control (13a) and ablated (13b) *P. homarus* under starvation

Appendix 13a

Source of variation	df	MS	F	P
Weeks of starvation	8	1.400	15.988	< 0.01
Residual	27	0.088		
Total	35			

Appendix 13b

Source of variation	df	MS	F	P
Weeks of starvation	6	4.604	49.036	< 0.01
Residual	21	0.094		
Total	27			

Appendix 14. Summary of ANOVA for the water content in the hepatopancreas of the control (14a) and ablated (14b) *P. homarus* under starvation

Appendix 14a

Source of variation	df	MS	F	P
Weeks of starvation	8	69.307	81.276	< 0.01
Residual	27	0.853		
Total	35			

Appendix 14b

Source of variation	df	MS	F	P
Weeks of starvation	6	113.393	117.057	< 0.01
Residual	21	0.969		
Total	27			

Appendix 15. Summary of ANOVA for the protein content in the hepatopancreas of the control (15a) and ablated (15b) *P. homarus* under starvation

Appendix 15a

Source of variation	df	MS	F	P
Weeks of starvation	8	22.269	40.125	< 0.01
Residual	27	0.555		
Total	35			

Appendix 15b

Source of variation	df	MS	F	P
Weeks of starvation	6	30.325	30.270	< 0.01
Residual	21	1.002		
Total	27			

Appendix 16. Summary of ANOVA for the lipid content in the hepatopancreas of the control (16a) and ablated (16b) *P. homarus* under starvation

Appendix 16a

Source of variation	df	MS	F	P
Weeks of starvation	8	51.726	147.222	< 0.01
Residual	27	0.351		
Total	35			

Appendix 16b

Source of variation	df	MS	F	P
Weeks of starvation	6	113.821	228.108	< 0.01
Residual	21	0.499		
Total	27			

Appendix 17. Summary of ANOVA for the carbohydrate content in the hepatopancreas of the control (17a) and ablated (17b) *P. homarus*

Appendix 17a

Source of variation	df	MS	F	P
Weeks of starvation	8	4.059	21.714	< 0.01
Residual	27	0.187		
Total	35			

Appendix 17b

Source of variation	df	MS	F	P
Weeks of starvation	6	1.685	4.704	< 0.01
Residual	21	0.358		
Total	27			

Appendix 18. Summary of ANOVA for the ash content in the hepatopancreas of the control (18a) and ablated (18b) *P. homarus* under starvation

Appendix 18a

Source of variation	df	MS	F	P
Weeks of starvation	8	19.285	65.202	< 0.01
Residual	27	0.296		
Total	35			

Appendix 18b

Source of variation	df	MS	F	P
Weeks of starvation	6	40.701	106.311	< 0.01
Residual	21	0.383		
Total	27			

Appendix 19. Summary of ANOVA for the energy content in the hepatopancreas of the control (19a) and ablated (19b) *P. homarus* under starvation

Appendix 19a

Source of variation	df	MS	F	P
Weeks of starvation	8	12.833	43.023	< 0.01
Residual	27	0.298		
Total	35			

Appendix 19b

Source of variation	df	MS	F	P
Weeks of starvation	6	26.458	115.342	< 0.01
Residual	21	0.229		
Total	27			

Appendix 20. Summary of ANOVA for the water content in the exoskeleton of the control (20a) and ablated (20b) *P. homarus* under starvation

Appendix 20a

Source of variation	df	MS	F	P
Weeks of starvation	8	0.266	1.020	> 0.05
Residual	27	0.261		
Total	35			

Appendix 20b

Source of variation	df	MS	F	P
Weeks of starvation	6	0.290	0.763	> 0.05
Residual	21	0.380		
Total	27			

Appendix 21. Summary of ANOVA for the protein content in the exoskeleton of the control (21a) and ablated (21b) *P. homarus* under starvation

Appendix 21a

Source of variation	df	MS	F	P
Weeks of starvation	8	0.978	36.633	< 0.01
Residual	27	0.027		
Total	35			

Appendix 21b

Source of variation	df	MS	F	P
Weeks of starvation	6	1.043	52.349	< 0.01
Residual	21	0.020		
Total	27			

Appendix 22. Summary of ANOVA for the lipid content in the exoskeleton of the control (22a) and ablated (22b) *P. homarus* under starvation

Appendix 22a

Source of variation	df	MS	F	P
Weeks of starvation	8	1.634	35.208	< 0.01
Residual	27	0.046		
Total	35			

Appendix 22b

Source of variation	df	MS	F	P
Weeks of starvation	6	2.274	42.472	< 0.01
Residual	21	0.054		
Total	27			

Appendix 23. Summary of ANOVA for the carbohydrate content in the exoskeleton of the control (23a) and ablated (23b) *P. homarus* under starvation

Appendix 23a

Source of variation	df	MS	F	P
Weeks of starvation	8	0.845	19.208	< 0.01
Residual	27	0.044		
Total	35			

Appendix 23b

Source of variation	df	MS	F	P
Weeks of starvation	6	0.681	9.964	< 0.01
Residual	21	0.068		
Total	27			

Appendix 24. Summary of ANOVA for the ash content in the exoskeleton of the control (24a) and ablated (24b) *P. homarus* under starvation

Appendix 24a

Source of variation	df	MS	F	P
Weeks of starvation	8	4.145	1.113	> 0.05
Residual	27	3.723		
Total	35			

Appendix 24b

Source of variation	df	MS	F	P
Weeks of starvation	6	3.535	0.934	> 0.05
Residual	21	3.787		
Total	27			

Appendix 25. Summary of ANOVA for the energy content in the exoskeleton of the control (25a) and ablated (25b) *P. homarus* under starvation

Appendix 25a

Source of variation	df	MS	F	P
Weeks of starvation	8	0.001	4.634	< 0.01
Residual	27	0.0003		
Total	35			

Appendix 25b

Source of variation	df	MS	F	P
Weeks of starvation	6	0.001	3.606	< 0.05
Residual	21	0.0003		
Total	27			

Appendix 26. Summary of ANOVA for the protein-energy ratio in the muscle of the control (26a) and ablated (26b) *P. homarus* under starvation

Appendix 26a

Source of variation	df	MS	F	P
Weeks of starvation	8	0.0002	77.321	< 0.01
Residual	27	3.0×10^{-6}		
Total	35			

Appendix 26b

Source of variation	df	MS	F	P
Weeks of starvation	6	0.0003	113.377	< 0.01
Residual	21	0.03×10^{-6}		
Total	27			

Appendix 27. Summary of ANOVA for the protein-energy ratio in the hepatopancreas of the control (27a) and ablated (27b) *P. homarus* under starvation

Appendix 27a

Source of variation	df	MS	F	P
Weeks of starvation	8	0.0011	830.450	< 0.01
Residual	27	1.0×10^{-6}		
Total	35			

Appendix 27b

Source of variation	df	MS	F	P
Weeks of starvation	6	0.0019	338.375	< 0.01
Residual	21	6.0×10^{-6}		
Total	27			

Appendix 28. Summary of ANOVA for the protein-energy ratio in the exoskeleton of the control (28a) and ablated (28b) *P. homarus* under starvation

Appendix 28a

Source of variation	df	MS	F	P
Weeks of starvation	8	1.405	2.059	> 0.05
Residual	27	0.683		
Total	35			

Appendix 28b

Source of variation	df	MS	F	P
Weeks of starvation	6	5.019	1.329	> 0.05
Residual	21	3.778		
Total	27			